Biology of *Patanga japonica* (Orthoptera, Acrididae): Nymphal growth, host plants, reproductive activity, hatching behavior, and adult morphology

SEIJI TANAKA[1]

1 Matsushiro 1-20-19, Tsukuba, Ibaraki 305-0035, Japan

Corresponding author: Seiji Tanaka (stanaka117@yahoo.co.jp)

Abstract

The biology of *Patanga japonica* (Bolívar, 1898), including seasonal nymphal growth, host plants, mating, oviposition, hatching, and adult morphology, was studied under outdoor and indoor conditions in central Japan. A field census showed that this grasshopper had a univoltine life cycle and overwintered in the adult stage. Body size was found to increase with a delay in the time of adult emergence in females but not in males, and protandry was observed. The insects were mainly associated with a few plant species. Feeding tests showed that at least one of the 5 test nymphs molted to the second stadium on 37 plant species, and more than 50% did so on 23 plant species. Mating was frequently observed in April and May under outdoor conditions, and the daily maximum number of copulating pairs was positively correlated with air temperature. Copulatory behavior, including stridulation, is described in detail. Oviposition was frequently observed in May and June under outdoor conditions. Larger females produced more eggs per pod, and a negative relationship was observed between egg lengths and the number of eggs per pod, showing a trade-off. On average, female adults had 124 ovarioles. Egg hatching occurred at different times during the daytime, but the eggs from each pod hatched synchronously. Synchronous hatching was also observed in eggs kept in groups of 2, 4, and 10, but hatching occurred earlier in larger group sizes. Eggs achieved synchronous hatching by either delaying or advancing hatching time. Two eggs separated by several millimeters hatched less synchronously than those kept in contact with one another. However, similarly separated eggs restored hatching synchrony when connected by thin wire, suggesting the involvement of vibrational signals in embryo–embryo communication. Morphometric analysis suggested that *P. japonica* adults change some morphometric ratios in response to crowding. Variation in pronotum shape was not significantly affected by crowding.

Keywords

Introduction

The grasshopper, *Patanga japonica* (Bolívar, 1898) (also known as *Nomadacris*), is widely distributed in Asia, including Japan, Korea, Taiwan, China, Vietnam, and India (Cigliano et al. 2022). In subtropical regions, including Okinawa Prefecture, it has a univoltine life cycle and overwinters in the adult stage (Tanaka and Okuda 1996). This and another large grasshopper, *Patanga succincta* (Johannson, 1763), are often found in the same sugarcane fields and adjacent areas in subtropical regions. In the temperate region of Japan, *P. japonica* is the only grasshopper known to overwinter as an adult (Ichikawa et al. 2006, Murai and Ito 2011). Nymphs and adults have been observed feeding on the Kudzu, *Pueraria montana* var. *lobata* (Willd.) Sanjappa and Pradeep, and the Japanese hop, *Humulus scandens* (Lour.) Merr., as well as species of Poaceae (Ichikawa et al. 2006). However, the range of host plants is poorly known. Although it is a common species, it is not an economically important grasshopper and has received little attention from researchers, except for some morphological and physiological studies (Okuda et al. 1996, Tanaka and Okuda 1996, Nakamori and Sadoyama 2001). Having obtained various information in the laboratory on *P. japonica* (Tanaka and Okuda 1996, Okuda et al. 1996), I became interested in studying this species in the field. To understand the significance of morphological, behavioral, and physiological variations in an insect, it is important to obtain basic knowledge about its biology, particularly its seasonal life cycle and behavior in the field.

The purpose of the present study was to describe the biology of *P. japonica*, including seasonal development, host plants, mating, oviposition, and hatching behavior, in central Japan. I recorded the plants on which nymphs and adults stayed during the growing season to determine whether there was a difference in the plants

used by the two stages. I also conducted indoor feeding tests of 51 species of plants found in the habitats of this grasshopper to determine the host range. In mating behavior, the copulating posture and stridulating behavior were observed in detail. By rearing adults under outdoor conditions, the number of egg pods laid by females and the length of the oviposition season were determined. I also measured egg pod size and examined its relation to the number of eggs contained as well as the relationships between the number of eggs, egg size, number of ovarioles, and body size of the female parent. I confirmed that nymphs of this grasshopper hatched in synchrony and focused on the mechanism controlling hatching synchrony, with particular attention paid to embryo–embryo communications. Finally, I tested whether this grasshopper exhibited density-dependent variation in adult morphometric traits as often observed in other grasshoppers and locusts (Uvarov 1966, 1977, Pener 1991, Pener and Yerushalmi 1998, Pener and Simpson 2009). In this paper, I describe the results of these observations and discuss the characteristics of this grasshopper.

Materials and methods

Field census.—The number of *P. japonica* individuals was recorded in a grassy area in Tsukuba, Ibaraki prefecture (36.1°N, 140.1°E), in Japan every week from July to November, except for the week of September 2 in 2021. The grasses were cut short on June 29 and October 30 by the government of the city of Tsukuba. The study site was adjacent to a pedestrian road and measured approximately 2 m by 200 m. As I walked slowly along this area, I visually counted grasshoppers and identified their developmental stages. It usually took 30–60 minutes to finish each census. For the first four stadia, personal experience made visual identification of nymphal stadia relatively easy: nymphal body length and head

width increased as nymphs grew bigger (Figs 1, 2). In this paper, I use 'stadium' to count the nymphal stages from hatching and 'instar' to describe the penultimate and last nymphal stages that can be identified by the characteristic wing pads. The process for measuring the body lengths of nymphs was as follows: Nymphs were reared singly on cut leaves of *Echinochloa crus-galli* (L.) P. Beauv. in plastic cups (9 cm in diameter, 4.5 cm in height) set near a window and kept at room temperature. A few days after each molt, each nymph was put in a transparent plastic bag, and the body length from the head to the tip was measured with a digital caliper to the nearest 0.1 mm (Digipa pro; Mitsutoyo Co., Kanagawa, Japan). After the fourth stadium, most fifth-stadium nymphs developed wing pads on the dorsal body surface by which they could easily be identified as penultimate instars (Fig. 1E). They molted to the last instar with larger wing pads (Fig. 1F). Adult stage was attained after the sixth stadium. Preliminary observations indicated that some female fourth-stadium nymphs went through an additional stadium and reached the penultimate instar at the sixth stadium (Suppl. material 1). Thus, this grasshopper passes 6 or 7 nymphal stadia before the adult stage. In the field, however, it was not possible to identify the nymphal stadium of the last two stadia with certainty. Therefore, in this census, nymphs at the last two stadia were identified as the penultimate and last instars, respectively, based on their wing pad sizes. Thus, it was likely that individuals without penultimate wing pads at the fifth stadium were included in the category of fourth-stadium nymphs.

Host plants.—During the above census, I recorded the plant species on which nymphs and adults were feeding or sitting. Because feeding activities are not easily observed in the field, these plants do not necessarily represent the host plants of this grasshopper. To solve this problem, I collected 51 species of plants found in
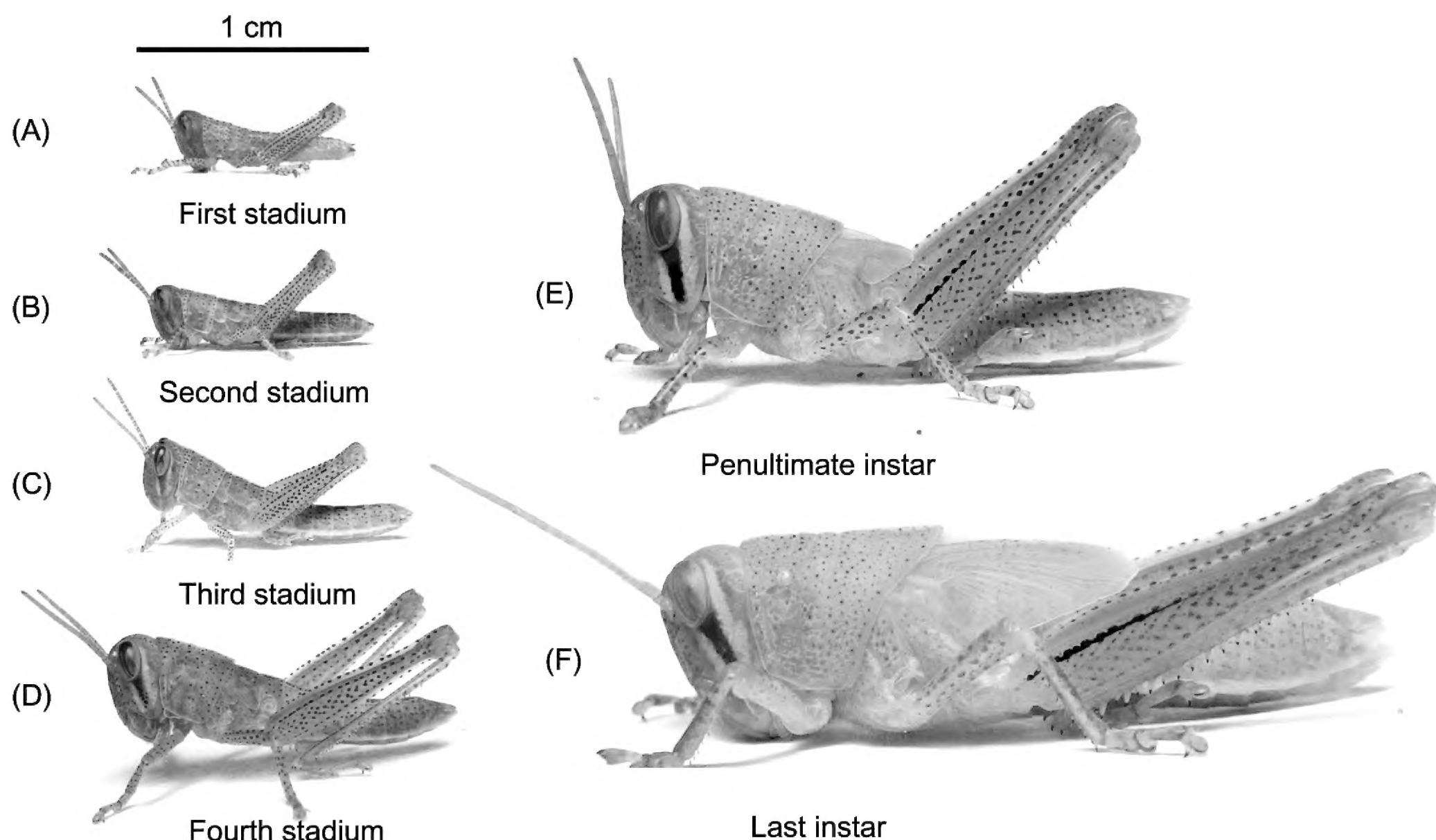

1 cm

(A) First stadium

(B) Second stadium

(C) Third stadium

(D) Fourth stadium

(E) Penultimate instar

(F) Last instar

Fig. 1. Nymphal growth of *Patanga japonica*. First to fourth stadia (**A–D**). Penultimate (**E**) and last (**F**) instars are characterized by wing pads.
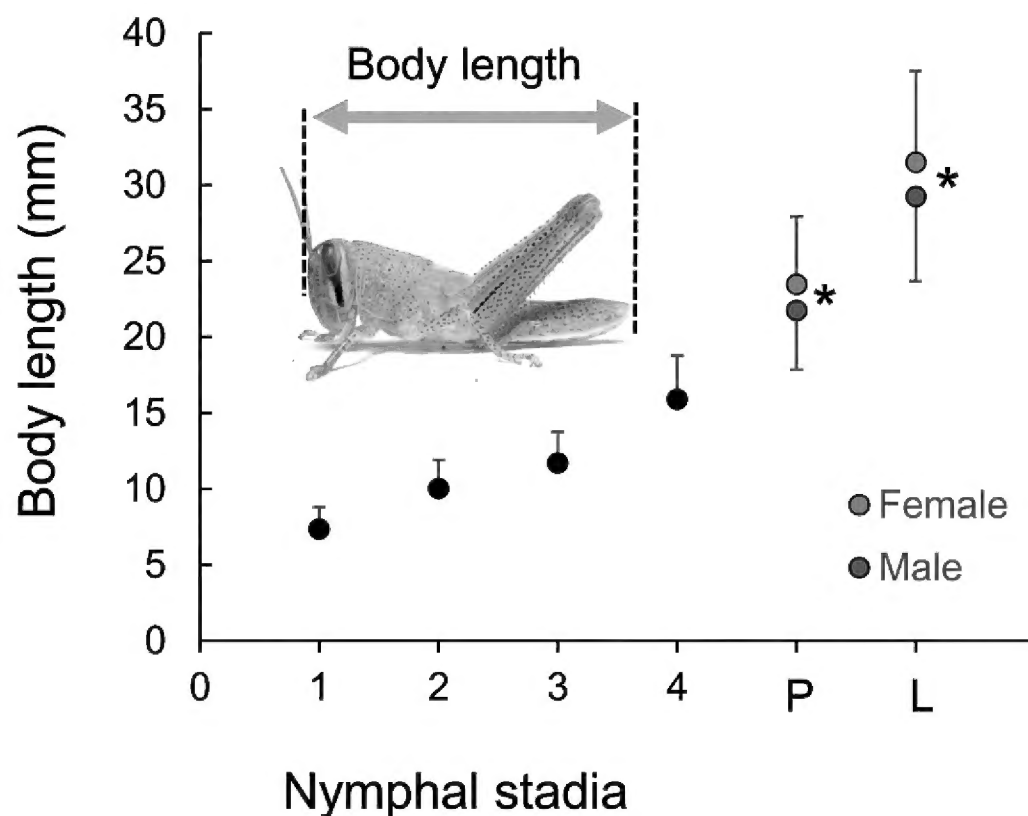
Fig. 2. Changes in body length (mean + or - SD, N = 20 each) during nymphal development in *Patanga japonica*. Asterisks indicate a significant difference between sexes by *t*-test ($p < 0.001$). P, penultimate instar; L, last instar.

their habitats, including the study site, and determined if nymphs would feed and grow while eating them. Five newly hatched nymphs were kept with pieces of leaves from each plant in a plastic cup (9 cm in diameter, 4.5 cm in height) covered with a perforated lid. Plant leaves were replaced by fresh ones every day. The nymphs kept with appropriate host plants molted to the second stadium in 5–7 days at room temperature, whereas those kept with a moist cotton ball alone died on the third day without molting. No cannibalism was observed.

Mating.—To determine when mating begins in the spring and to observe the mating behavior of *P. japonica*, 10 female and 10 male adults collected in the field were housed in a wood-framed enclosure (50 × 80 × 30 cm, Suppl. material 2A) on the litter ground in Tsukuba on February 4, 2022 and fed with cut leaves of *Bromus catharticus* Vahl held in a jar of water. The walls of the enclosure were covered with nylon mesh, and the top was covered with a glass plate during the day for observation and with nylon mesh during the night for natural ventilation and rainfall. All adults were marked on the thorax and forewing with different paint colors for identification and usually checked for copulation every 1 or 2 h from 08:00 to 18:00. Most mounting males were copulating. Temperature on the litter floor was recorded every hour with a thermo recorder (TR-52i, Ondotori Jr., T & D Co. Nagano, Japan).

Grasshoppers generally copulate in a characteristic fashion (Uvarov 1966). Typically, the male sits on the back of the female and copulates by curving down his abdomen to reach her genitalia. In this case, the male bends his abdomen either from the right or left side of the female body. In *P. japonica*, I examined this phenomenon by observing adults in cages mainly during the day. On some nights, I observed their behavior using a red LED lamp. To examine whether this behavior was controlled by males or females, I changed their partner.

Oviposition.—Oviposition activity was observed for 20 pairs of a female and a male housed in small cages (28 × 12 × 28 cm; Suppl. material 2B) and a group of 10 females and 10 males housed in a large cage (42 × 22 × 42 cm) in 2021. The air temperatures re-

corded at Tsuchiura, Ibaraki (36.06N, 140.13E), during the observation period were obtained from the Japan Meteorological Agency (2022). A plastic cup (10 cm in diameter, 5.5 cm in height) filled with moist sand (approximately 15% water by volume) was placed in each cage and checked for egg pods every day. The cups containing egg pods were kept at 30 ± 1°C in an incubator (CN-40A; Mitsubishi Electric Engineering Co., Tokyo, Japan) for 1 or 2 days, and the egg pods were washed in chlorinated tap water to remove sand. The maximum width and length of the egg pods were then measured with a digital caliper and held in moist sand in plastic cups (100 ml in volume) for incubation (30 ± 1°C). The eggs of 5 egg pods incubated at this temperature took 30.0 days to hatch (SD = 0.7 days; N = 271). Four or five days before the expected day of hatching, the number of eggs contained in each pod was counted, and the lengths of 10 eggs taken from each pod were measured with a digital caliper under a binocular microscope. The number of ovarioles was counted for 16 female adults collected in the fall by dissecting one ovary from each female under a binocular microscope. The number multiplied by two was regarded as the number of ovarioles for each female.

Hatching.—Hatching time was determined under semi-outdoor conditions in June 2021. Egg pods that were expected to hatch within 4–5 days at 30°C were buried at a depth of 2–5 cm in soil held in a plastic washtub (50 cm in diameter, 25 cm in height). They were covered with a transparent perforated cylinder (8.5 cm in diameter, 17 cm in height) covered with nylon mesh. The washtub was placed outdoors and photographed every 30 minutes with a digital camera to determine the hatching time (Suppl. material 2C). The number of hatched nymphs was calculated later on a computer. As described below, once hatching started, most eggs hatched within the same 30-minute period. Similar phenomena have been observed in the Eastern lubber grasshopper, *Romalea microptera* (Palisot de Beauvois, 1817) (Smith et al. 2013) and the Western lubber grasshopper, *Taeniopoda eques* (Burmeister, 1838) (Whitman and Orsak 1985). Therefore, in this study, the start of hatching from an egg pod was regarded as the hatching time of each egg pod.

To confirm that synchronized hatching from the egg pods occurred at a constant temperature, the eggs were removed from each pod 10 days before the expected time of hatching, soaked in 6% sodium hypochlorite (Haiter, Kao Co., Tokyo) for 1 min to remove the pod material, and rinsed with tap water three times. Preliminary observations showed that this handling caused no detrimental influence on the hatching rate and time (Tanaka S, unpublished data). The eggs of each pod were then divided into two batches. The eggs in one batch were buried in a group of 10 or 20 eggs in a sand pit in a Petri dish (9 cm in diameter, 2 cm in height), and 10 or 20 eggs in the other batch were individually buried in sand pits in another dish, as previously described for the migratory locust, *Locusta migratoria* (Linnaeus, 1758) (Tanaka 2017), except that dark-colored river sand was used because the hatchlings were light green in color. The eggs were incompletely covered with sand, allowing them to receive light. They were incubated at 30 ± 1°C under continuous illumination and photographed from above every 30 minutes with a digital camera. The hatching time was determined as described above.

To examine the effect of group size on hatching, eggs from the same pod were divided into two batches of similar sizes that were then kept in groups of 2 versus 4 eggs or 4 versus 10 eggs at 30 ± 1°C under continuous illumination. Their hatching times were determined as described above. The effects of group size on the hatch-

ing time were compared by calculating the mean hatching times of different group sizes relative to the value for group size 10 that was designated as 1 h. Hatching intervals from the first to the last hatchings were also calculated. Only those egg groups with 100% hatching were used. Because photographs were taken at 30-minute intervals, 30 minutes was added to the differences in hatching times of eggs; therefore, 30 min was the minimum hatching interval.

The mechanism controlling hatching synchrony in *P. japonica* was examined by carrying out three experiments at 30 ± 1°C under continuous illumination using pairs of eggs according to the methods described for other grasshoppers (Tanaka 2017, 2021a, b).

In experiment 1, the effect of the presence of hatched nymphs on the hatching time of late-hatching eggs was tested by treating pairs of eggs in three different ways: 1) two eggs kept in contact with one another on sand in a well of a 24-well plate (Thermo Fisher Scientific KK, Tokyo, Japan), 2) two eggs kept separately with a distance of 2–5 mm, and 3) two eggs separated by a stainless wire screen (12 mm in length, 15.7 mm in width) that physically prevented the hatched nymph from touching the unhatched egg in the same well.

In experiment 2, whether vibrational stimuli are involved in inducing hatching synchrony or not was tested by placing pairs of eggs from the same egg pod horizontally on moist sand in wells of a 24-well plate in three different ways: 1) eggs kept in contact with one another, 2) eggs kept separated by 2–5 mm, and 3) eggs similarly kept separated but connected by two pieces of stainless wire (7 mm in length).

In experiment 3, I examined how eggs achieved hatching synchrony. In other words, does the hatching time of eggs advance or delay in response to stimuli from adjacent eggs? To answer this question, eggs from the same pod were divided into two batches 10 days before the expected date of hatching. One batch was incubated at 12–14°C for various lengths of time to suppress embryonic development and returned to 30°C, while the other batch was continuously kept at 30°C. Five days before hatching was expected to start, eggs from the respective batches were paired and placed together vertically in sand pits in wells of a 24-well plate as mixed pairs (12–14 pairs). In this case, care was taken to ensure that the two eggs were kept in contact with one another. Other eggs from the two batches were used as controls, each consisting of 6 or 7 pairs of eggs. The eggs in each control pair were buried individually in sand pits but kept in the same well. One control hatched earlier than the other, which are here called controls 1 and 2, respectively. The pits were incompletely covered with sand, allowing the eggs to receive light but preventing the nymph that hatched first from touching the unhatched egg. The hatching times were determined as described above, and the hatching intervals for the mixed and control pairs were calculated. The early and late hatching eggs in each mixed pair are referred to here as mixed eggs 1 and 2, respectively. Only those pairs in which both eggs hatched successfully were used for the analyses. In the three experiments, the hatching times were determined as described above, and the hatching intervals of eggs in pairs were calculated.

Morphometrics of adults grown under different conditions.—Adults of *P. japonica* were collected at the study site in October 2020 and March 2021. The density of individuals at this site was not measured precisely, but it is probably safe to say that it was lower than 1 per m². By following the method of Dirsh (1951, 1953), the maximum head width (C), hind femur length (F), and forewing length (E) of adults were measured using a digital caliper to the nearest 0.1 mm. My main interest was to determine if this grasshopper

would change its morphometric characters in response to crowding, as observed in locusts (Uvarov 1966, 1977, Pener 1991, Pener and Simpson 2009). According to previous studies on phase polyphenism in morphometric ratios in several locust species, such as *Schistocerca gregaria* (Forskål, 1775) and *Locusta migratoria* (Dirsh 1953, Farrow and Colless 1980, Sugahara et al. 2015, 2016), the F/C, E/F, and E/C ratios were adopted to assess the presence of density-dependent morphometric changes. Two experiments were carried out. One experiment compared the above parameters in field-collected adults (low density) and adults reared outdoors in a group (high density) in Tsukuba. Two groups of approximately 200 and 100 nymphs that hatched on July 5 and July 25, respectively, were reared in large cages. They fed on the leaves of *E. crus-galli*. In the other experiment, the parameters of adults reared individually in plastic containers (10 cm in diameter, 4.5 cm in height) and those reared in a group of 5 individuals per container or in a group of 50 individuals per large cage (high density) were compared. All insects were reared indoors (at room temperature and semi-natural daylengths) from June to August. Body dimensions were measured for the adults as described above. Additionally, the shape of pronotum, which is known to be another density-dependent character in *L. migratoria* (Uvarov 1966, Tanaka et al. 2002), was recorded for the indoor-reared adults. The ridge of the pronotum was recorded as arched, flat, or concaved according to the method of Tanaka (2022) for *L. migratoria*.

Statistical analyses.—The body size of *P. japonica* nymphs was compared between treatments using a *t*-test. The proportions of plant species were analyzed using a chi-squared test. Pearson's correlation coefficient and linear regression were used to analyze the relationships between egg number, egg length, and head width of female parents. Hatching rates were compared using a Mann–Whitney U test. Hatching intervals were compared using a Steel–Dwass test and a chi-squared test'. Hatching time was compared with Tukey's multiple comparison test. Adult dimensions and morphometric ratios were analyzed with Tukey's multiple comparison, a *t*-test, and a Steel–Dwass test. These analyses were performed using a statistics service available at http://www.gen-info.osaka-u.ac.jp/MEPHAS/kaiseki.html, Descriptive Statistics (Excel, Microsoft Office 365), or StatView (SAS Institute Inc., NC, USA). Differences were judged as significant when $p < 0.05$.

Results

Seasonal development.—*P. japonica* nymphs of different sizes, ranging from first stadium to penultimate instar, were observed on July 29, 2021, when the census was begun (Fig. 3). My observations suggested that hatching started in early July, which was confirmed in 2022, when 88.2% of the nymphs observed at the site were at the first stadium and 11.8% and 4.1% were second and third stadium nymphs, respectively, on July 7 (N = 43, Tanaka, S. unpublished observation). Nymphs grew gradually as the season advanced, and adults began to be seen on September 16, with only adults observed on November 24. On October 30, the grasses at the study site were cut and removed, which caused most grasshoppers to move to adjacent bushes or to be killed.

To observe the pattern of adult emergence, nymphs that hatched on July 5 were reared in a cage under outdoor conditions. Adults started appearing on September 5, and the mean duration of nymphal development was 76.0 days (SD = 6.1, N = 46) and 81.6 days after hatching (SD = 5.9, N = 67) in males and females, respectively, which corresponded to September 19 and 25 (Fig. 4).
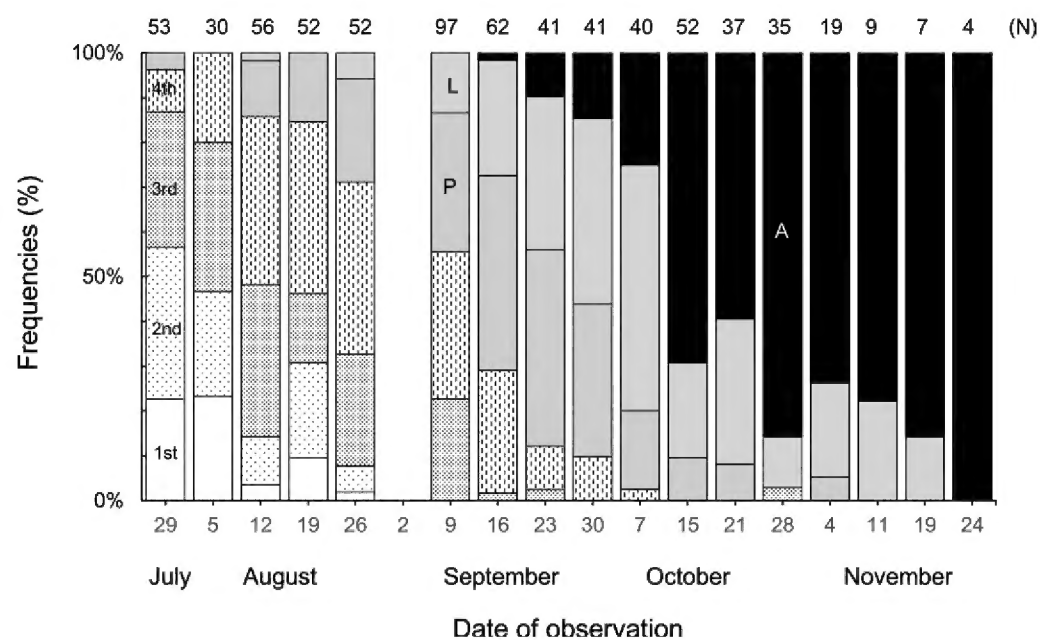
Fig. 3. Seasonal changes in nymphal development in *Patanga japonica* in Tsukuba in 2021. For nymphal stadia and instars, see Fig. 1. 1st–4th, stadia; P, penultimate instar; L, last instar; A, adult.
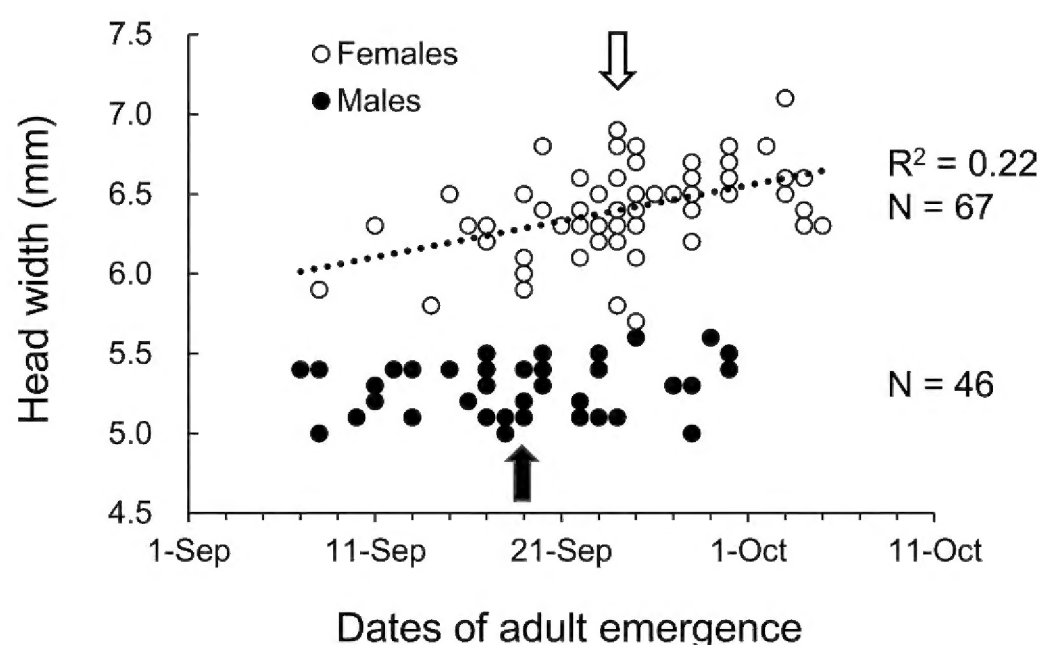

Fig. 4. Seasonal changes in adult head width in *Patanga japonica* individuals that hatched on July 5 in 2021 and were reared outdoors in a group. Arrows indicate the mean time of adult emergence.

No significant sex difference was observed in variance (*F*-test, $p = 0.41$). On average, males emerged as adults 5.6 days earlier than females ($t = 4.86$; DF = 111, $p < 0.001$), indicating the presence of protandry. Female adults showed a significant increase in body size with delay in the time of adult emergence ($r = 0.46$, $p < 0.001$, Fig. 4), while no significant correlation was observed between the two variables in males ($r = 0.22$, $p = 0.14$).

Plants used by P. japonica.—Fig. 5 compares the plants on which grasshoppers were observed. Nymphs mainly stayed on the leaves of three plant species—(92.7%) *Pueraria montana* var. *lobata* (Willd.) Maesen & S.M. Almeida ex Sanjappa & Pradeep, *Miscanthus sinensis* Andersson, and *Imperata cylindrica* (L.) P. Beauv. *a*—representing 66.3%, 12.0%, and 14.4%, respectively (N = 409). The corresponding figures for adults were 56.2%, 10.0%, and 9.2% (N = 130). The remaining 24.6% of adults were observed on various other plants. The composition of the four categories in Fig. 5 was significantly different between nymphs and adults ($\chi^2 = 29.5$, DF = 1, $p < 0.01$). Both nymphs and adults of this grasshopper were frequently observed making holes in the leaves of *P. montana var. lobata* rather than feeding on them from the edges (Suppl. material 2D).

The above results do not necessarily indicate that grasshoppers feed on those plants. To examine the range of host plants of *P. japonica*, newly hatched nymphs were held with leaves of various plant species and observed until they molted to the 2nd stadium or died without molting. All nymphs kept with only a moist cotton ball died on the third day. Out of the 51 plant species tested, 37 (72.5%) belonging to 16 families led at least one *P. japonica* nymph to attain the following stadium (Table 1). All nymphs reached the 2nd stadium on 7 plant species, and more than 50% of nymphs (3–5 nymphs) did so on 23 plant species belonging to 10 different families. The results suggest that *P. japonica* could use a wide range of plant species for development.

Mating.—In 2021, the first mating pair among adults kept in an outdoor cage was observed on March 14. In 2022, the first mating was observed in an outdoor cage on March 19, and the second one was observed on April 2 (data not shown). Mating was frequently observed in April and May (Fig. 6A) in 2022 and was continuously observed until late July, when a few adults were still alive (data not shown). In the field, the last male was collected on July 7, 2021. In 2022, the last male and female were captured at the study site on July 7 and August 10, respectively. The latter laid an egg pod 3 days later and then died.

From April 2 to May 13, copulation was observed on a total of 26 days (Fig. 6A), and the mean number of copulating pairs was positively correlated with the time of day within the observed range (Fig. 6B). The number of copulating pairs gradually increased from 08:00 to 14:00 and leveled off thereafter. The daily maximum number of copulating pairs showed a higher correlation with the mean temperature of the day ($r = 0.39$, N = 41, $p < 0.01$) than with that from 08:00 to 18:00 ($r = 0.32$, N = 41; $p < 0.05$) or from 10:00 to 16:00, during which the temperature tended to be high due to sunshine ($r = 0.27$, N = 41, $p = 0.09$, Fig. 6C). Few observations were made between 18:00 and 8:00, during which the mean number of copulating pairs decreased by 41.9% from 2.96 to 1.72 (Fig. 6B, $t = -2.50$, DF = 44, $p < 0.05$).

The length of copulation was not precisely determined in this study. Some adults were found copulating at 8:00 when observations started each day, and mating ended 1–14 h later (Suppl. material 3). However, many pairs (42 pairs, 71.2%) remained without separating at the end of the daily observation (18:00–22:00, Suppl. material 3), and some continuously remained copulating for a few days, although the possibility that they separated during the night and mated again in the morning could not be ruled out completely.

In *P. japonica*, the male copulated with the female by bending his abdomen either from the right or left side of her body to reach her genitalia (Suppl. material 2E). The frequencies of males copulating from the right and left sides were 31 and 35, respectively, and their proportions did not significantly deviate from unity ($\chi^2 = 0.12$, DF = 1, $p > 0.05$). Some males were moved to another cage to allow them to mate with a second female to determine whether the bending direction was fixed or changeable depending on the partner. Of a total of 26 males tested during the period from May 19 to June 18 in 2022, 16 were observed copulating with two different females from the same side, although some of these females (N = 11) had previously copulated with a male bending his abdomen from the opposite side. These results suggest that the side of the female that was used for copulation depended on the male.

P. japonica adults were seen to stridulate by rubbing their abdomens or forewings with the hind tarsi. The stridulation was usually repeated 3 or 4 times each time using one leg (Suppl. material 4). This behavior was displayed almost exclusively by males, with one exception: one female stridulated by moving both legs alternately on the floor of a cage. In males, this behavior was observed only during copulation, suggesting that it was not for calling a female. In group-rearing, a copulating pair was often surrounded by other males, but
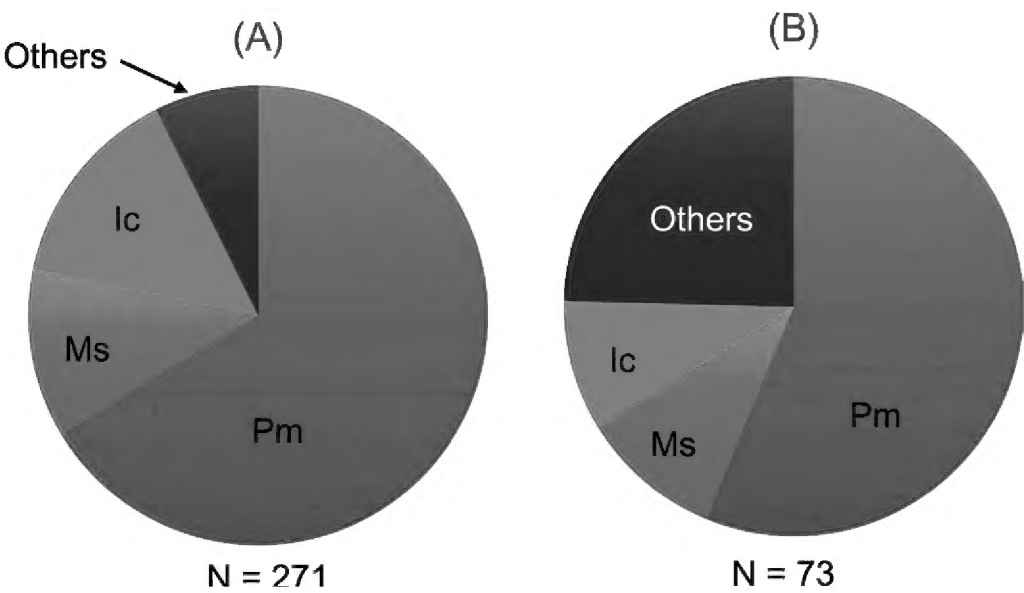
Fig. 5. Composition of plant species on which *Patanga japonica* nymphs (**A**) and adults (**B**) were observed. Pm, *Pueraria montana var. lobata*; Ms, *Miscanthus sinensis*; Ic, *Imperata cylindrica*.
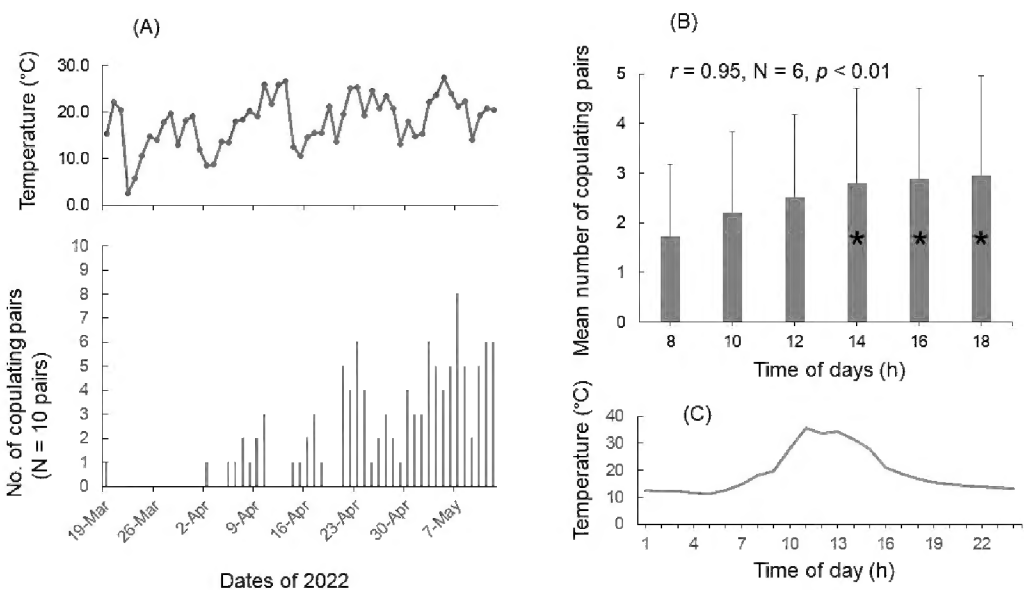

Fig. 6. Mating activity of *Patanga japonica* observed outdoors in a wood-framed enclosure in 2022. **A.** Daily mean air temperatures and number of copulating pairs; **B.** Mean number (+ SD) of copulating pairs at different times of day; C. Mean temperature on the litter floor.

male–male physical competition for a female appeared to be rare. I did not encounter a situation in which a male took over and copulated with the female by physically fighting the mounting male.

It was also noticed that a male reaching the female genitalia from the left (right) side used his right (or left) leg to stridulate. To determine whether such a relationship was a rule, copulating pairs were checked once a day from April 10 to May 2 in 2022. As expected, 62 males (93.9%) followed the above rule, while 4 males used both legs to stridulate. In the latter mating pairs, the females tilted their body by approximately 30 degrees to orient it toward the sun (Suppl. material 5). As a result, it was possible that the males had difficulty in stridulating using their leg on the appropriate side. After bathing ended, these males stridulated using the 'appropriate' leg as observed in the other males.

In another observation carried out from April 17 to May 4 in 2022, 8 males with a missing hindleg were paired with an intact female to test the hypothesis that these males would copulate by bending their abdomen from the same side as that of the missing leg. The female partner was changed every day. The above hypothesis was supported by all but one case (N = 20).

Oviposition.—Oviposition started on April 27 and continued until August 1 in 2021 under outdoor conditions (Fig. 7). Oviposition intervals were 10.4 days on average (range = 4–22, N = 98, Suppl. material 6A). High oviposition activities were observed on warm

Table 1. Number of hatchlings that molted to the 2nd stadium when five hatchlings were kept at room temperature with various plant species taken from habitats of *Patanga japonica*.

| No.	Plant species	Family	No. of nymphs that molted to 2nd stadium
1	*Chenopodium album* L. var. *centrorubrum* Makino	Amaranthaceae	5
2	*Humulus scandens* (Lour.) Merr.	Cannnabaceae	5
3	*Trifolium repens* L.	Fabaceae	5
4	*Trifolium pratense* L.	Fabaceae	5
5	*Bromus catharticus* Vahl (1791)	Poaceae	5
6	*Digitaria ciliaris* (Retz.) Koel	Poaceae	5
7	*Echinochloa crus-galli* (L.) P. Beauv.	Poaceae	5
8	*Achyranthes bidentata* Blume var. *japonica* Miq.	Amaranthaceae	4
9	*Cyperus microiria* Steud.	Cyperaceae	4
10	*Pueraria montana* var. *lobata* (Willd.) Maesen & S.M. Almeida ex Sanjappa & Pradeep	Fabaceae	4
11	*Perilla frutescens* (L.) Britton var. *acuta* (Thunb.) Kudô	Lamiales	4
12	*Eleusine indica* (L.) Gaertn.	Poaceae	4
13	*Dactylis glomerata* L.	Poaceae	4
14	*Setaria viridis* L.) P. Beauv.	Poaceae	4
15	*Miscanthus sinensis* Andersson (1855)	Poaceae	4
16	*Imperata cylindrica* (L.) P. Beauv.	Poaceae	4
17	*Rumex acetosa* L.	Polygonaceae	4
18	*Erigeron annuus* (L.) Pers.	Asteraceae	3
19	*Taraxacum officinale* Weber ex F.H. Wigg. (1780)	Asteraceae	3
20	*Commelina communis* L.	Commelinaceae	3
21	*Equisetum arvense* L.	Equisetaceae	3
22	*Lespedeza bicolor* Turcz. (1840)	Fabaceae	3
23	*Lolium multiflorum* Lam.)	Poaceae	3
24	*Lactuca indica* L.	Asteraceae	2
25	*Artemisia indica* Willd Willd. var. *maximowiczii* (Nakai) H.Hara	Asteraceae	2
26	*Galinsoga quadriradiata* Ruiz et Pav.	Asteraceae	2
27	*Trichosanthes cucumeroides* (Ser.) Maxim. ex Franch. et Sav.	Cucurbitaceae	2
28	*Aeschynomene indica* L.	Fabaceae	2
29	*Desmodium paniculatum* L.	Fabaceae	2
30	*Cocculus orbiculatus* L.	Menispermaceae	2
31	*Plantago asiatica* L.	Plantaginaceae	2
32	*Persicaria longiseta* (Bruijn) Kitag.	Polygonaceae	2
33	*Houttuynia cordata* Thunb. (1783)	Saururaceae	2
34	*Solanum nigrum* L.	Solanaceae	2
35	*Erigeron annuus* L.	Asteraceae	1
36	*Cirsium japonicum* Fiscb. Ex DC.	Asteraceae	1
37	*Rumex japonicus* Houtt.	Polygonaceae	1
38	*Rhus javanica* L.	Anacardiaceae	0
39	*Erigeron annuus* (L.) Pers.	Asteraceae	0
40	*Bidens biternata* (Lour.) Merr. et Sherff	Asteraceae	0
41	*Solidago canadensis* var. *scabra* L.	Asteraceae	0
42	*Conyza canadensis* (L.) Cronquist	Asteraceae	0
43	*Dioscorea japonica* Thunb. (1784)	Dioscoreaceae	0
44	*Lespedeza juncea* (L.fil.) Pers. var. *subsessilis* Miq.	Fabaceae	0
45	*Oenothera biennis* L.	Onagraceae	0
46	*Oenothera rosea* L'Hér. ex Aiton	Onagraceae	0
47	*Xanthoxalis corniculata* (L.) Small	Oxalidaceae	0
48	*Phytolacca americana* L.	Phytolaccaceae	0
49	*Paederia scandens* (Lour.) Merr.	Rubiaceae	0
50	*Smilax china* L.	Smilacaceae	0
51	*Cayratia japonica* Gagn.	Vitaceae	0
52	Cotton ball moistened with tap water		0
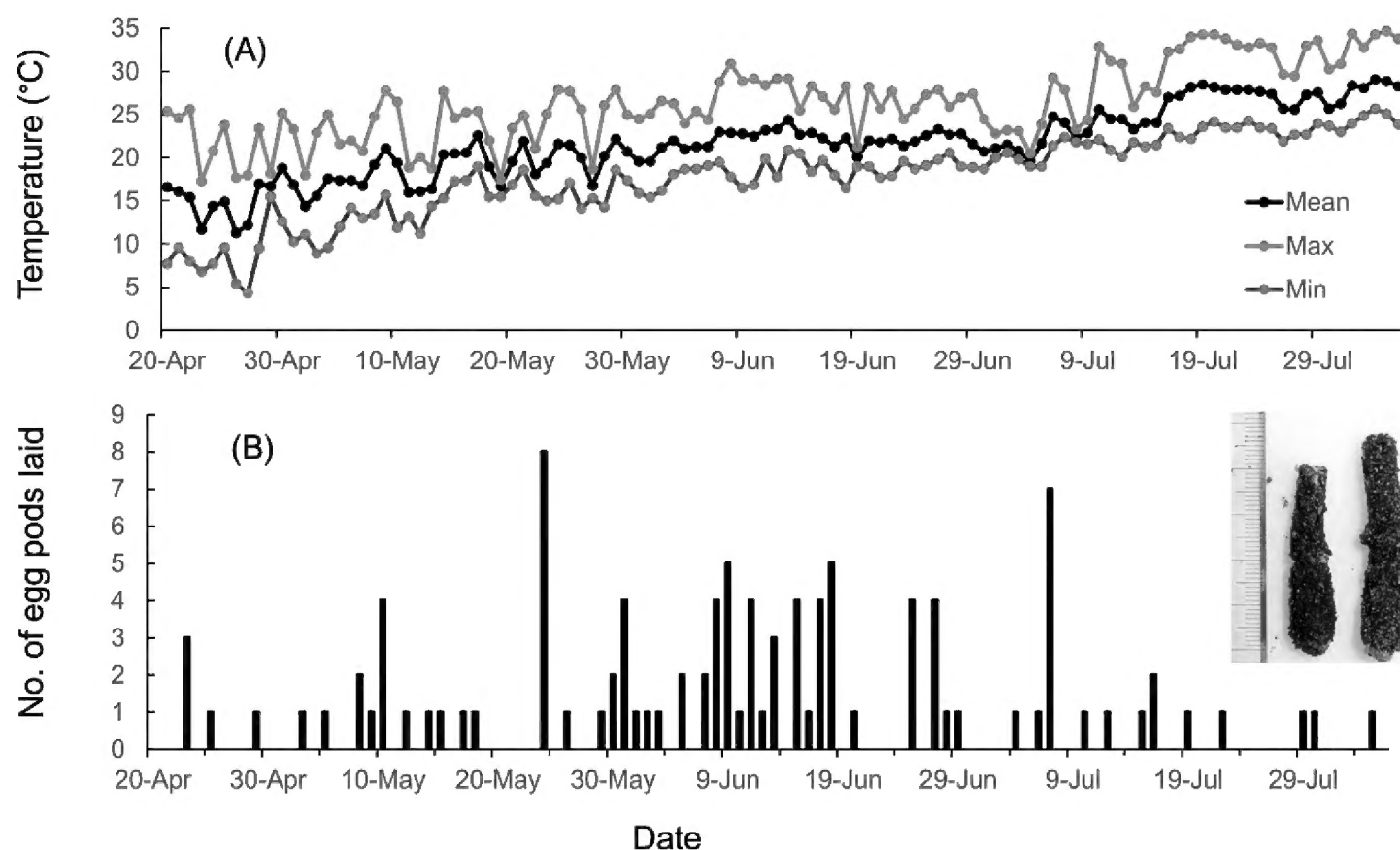
Fig. 7. Air temperatures (**A**) and daily number of egg pods laid by *Patanga japonica* in outdoor cages in 2021 (**B**). Inset shows egg pods. Air temperatures are derived from the Japan Meteorological Agency (2022).
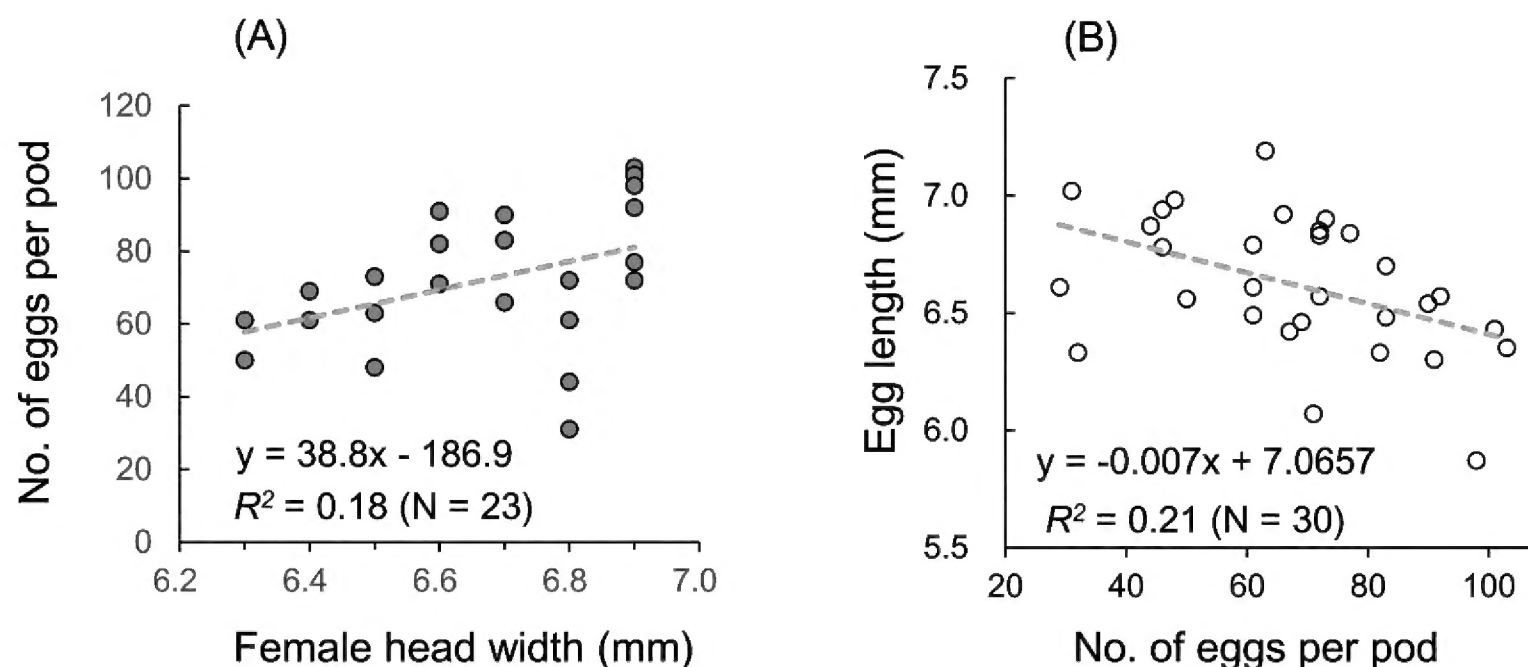

Fig. 8. Relationships between female head widths and numbers of eggs per pod (**A**) and between number of eggs per pod and egg lengths (**B**) in *Patanga japonica*.

days. Half of the females deposited their last egg pod by early July, and most females ceased oviposition by the end of July (Suppl. material 6B). As mentioned earlier, the female collected on August 10 in the field in 2022 laid her last egg pod on August 13 and died the following day. Females laid 5.4 egg pods on average (SD = 2.7 pods, range = 0–9 pods, N = 20). Egg pods were 9.1 mm wide (SD = 0.8 mm, range = 1.2–0.7, N = 99) and 60.7 mm long on average (SD = 16.5 mm, range = 91.0–30.3, N = 74).

The average number of ovarioles was 123.5 (SD = 14.7, N = 16) and showed no significant correlation with head width ($r = 0.09$, $p > 0.05$). The average number of eggs per pod was 72.1 (SD = 18.9, range = 44–103, N = 23). The lifetime fecundity, which was estimated by multiplying the number of egg pods produced by the number of eggs per pod, was 446.8 on average (range = 144–904 eggs, N = 11).

A significant positive correlation was observed between the numbers of eggs per pod and the head widths of the female parents (Fig. 8A; $r = 0.42$, N = 23, $p < 0.05$), suggesting that larger females tended to produce more eggs per pod. A significant negative correlation was observed between the number of eggs per pod and egg length (Fig. 8B; $r = –0.46$, N = 30, $p < 0.05$), suggesting a trade-off between the two traits. In contrast, the correlation between

adult head width and egg length was statistically insignificant ($r = –0.11$, N = 11), probably because the sample size was small. Lifetime fecundity was not significantly correlated with adult head width ($r = 0.12$, N = 11, $p = 0.71$).

Egg pods produced by adults that were reared in a group of 5 females and 5 males after collection in March contained significantly fewer eggs (mean = 53.6, SD = 20.7, N = 7) than those produced by females kept with a single male (mean = 72.16, SD = 18.1, N = 23, $t = 2.23$, DF = 28, $p < 0.05$). However, there was no significant difference in egg length between egg pods produced by the two groups of females [mean = 6.6 mm, SD = 0.2 mm, N = 7 for eggs laid by group-reared females; mean = 6.6 mm, SD = 0.3 mm, N = 23 for egg pods laid by females kept with a male (*t*-test, $p > 0.05$)].

Hatching under outdoor conditions.—Once hatching started under outdoor conditions, most nymphs hatched from the egg pod within 30 minutes (Fig. 9A). Because hatching from the egg pod occurred simultaneously, the start of hatching identified by interval photographing was regarded as the time of hatching for each egg pod. Egg hatching occurred at different times of day between 10:45 and 18:30 (Fig. 9B). No eggs hatched during the night.
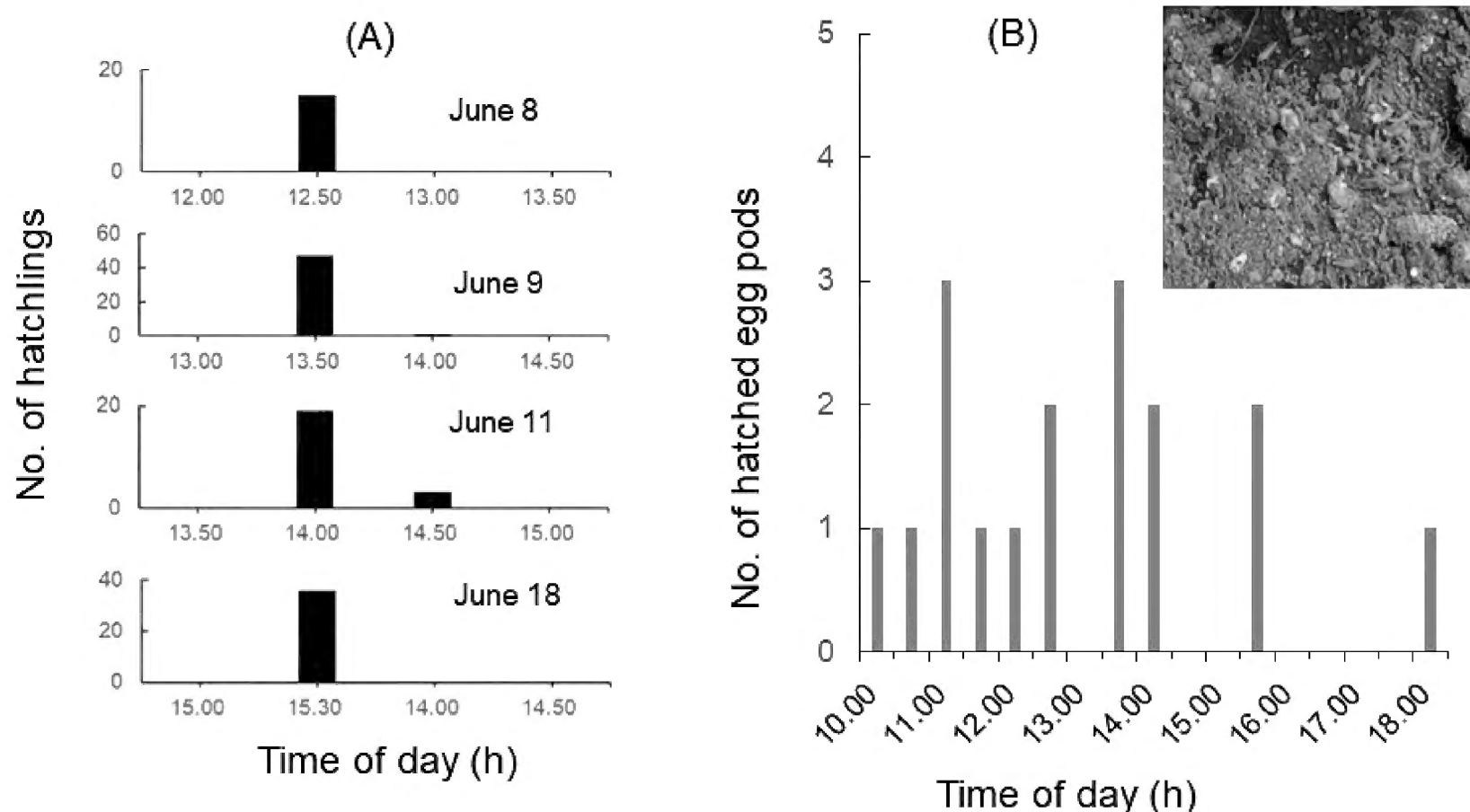
Fig. 9. *Patanga japonica* egg hatching. **A.** Hatching time from 4 egg pods; **B.** Number of egg pods that hatched at different times of the day. Inset in (**B**) shows simultaneous hatching from the egg pod.
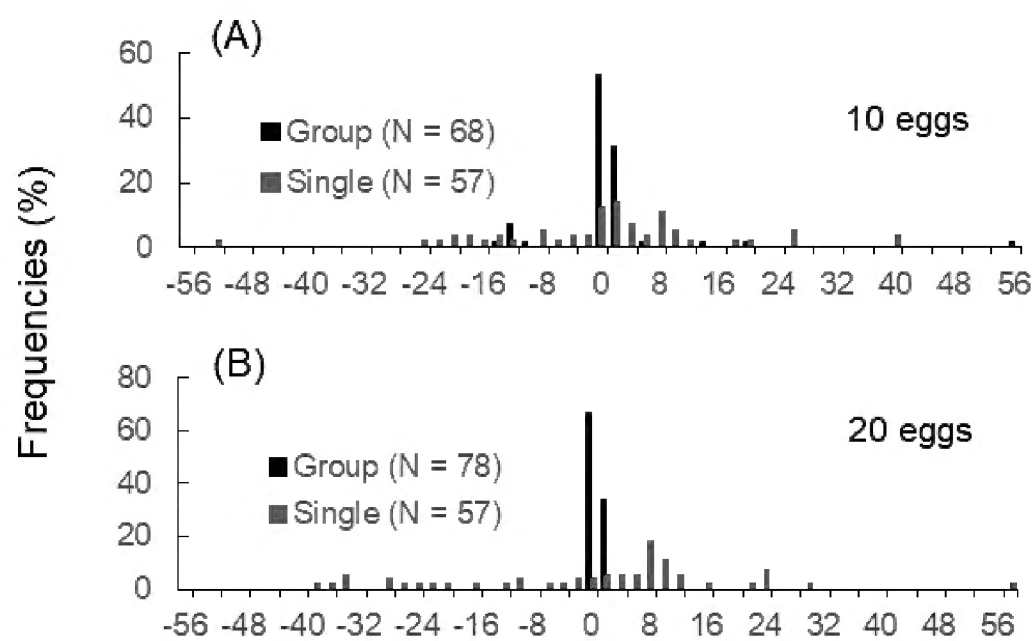

Fig. 10. Hatching distribution of *Patanga japonica* eggs kept singly and those kept in a group of 10 (**A**) and 20 (**B**) at 30°C when the mean hatching time was adjusted to 0 h. *F*-test shows that the variances of two treatments are significantly different from one another ($p < 0.05$).

Mechanism controlling hatching synchrony.—To confirm the presence of synchronous hatching under controlled conditions, the pattern of hatching was compared between eggs kept in a group and those kept singly. Fig. 10 shows that most eggs kept in a group of 10 or 20 eggs hatched within 1 h of the mean hatching time (0 h), with the SD being 0.8 h and 0.2 h, respectively, whereas those kept singly hatched over a wider range of time, with the SD being 15.3 h and 19.0 h. The mean hatchability of pooled data for the eggs kept in a group and those kept singly was 97.1% and 78.1%, respectively, and the difference was statistically significant (Mann–Whitney *U*-test, $z = 3.15$, N = 11 each, $p < 0.05$).

Hatching tended to occur earlier in eggs kept in a larger group in a sand pit (Fig. 11A). The mean hatching interval between the first and last hatching was similar among the three groups ($p > 0.05$, Steel–Dwass test, Fig. 11B). The proportion of pairs with hatching intervals ≤ 1h also showed no significant difference between the three treatments ($\chi^2 = 0.56$, DF = 2, $p > 0.05$).

Two eggs kept in contact with one another hatched more synchronously than those kept separated by 2–5 mm on sand (Fig. 12A; Steel–Dwass test, $p < 0.05$). The hatching interval of the two eggs was further prolonged if an early hatched nymph was prevented from touching the other egg by a mesh separator. Hatching time was significantly delayed when two eggs were isolated by a mesh separator (Fig. 12B; Tukey's multiple test, $p < 0.05$).

Two eggs separated by 2–5 mm showed a significantly wider mean hatching interval (6.9 h) than those kept in contact with one another (1.6 h; Fig. 13A, B; Steel–Dwass test, $p < 0.05$). In contrast, separated eggs hatched as synchronously as those kept in contact with one another when they were connected by two pieces of wire (2.4 h; Fig. 13A, C; $p > 0.05$), suggesting that some physical stimuli transmitted via the wire facilitated synchronous hatching.

To determine how hatching synchrony was achieved between eggs, the contents of 14 egg pods were divided into two batches of eggs, and one batch was chilled in a refrigerator for various lengths of time, and the other batch was continuously kept at 30°C. One egg was taken from each of the two batches and put together as mixed pairs in a sand pit (mixed pair) or buried individually as controls at 30°C (Fig. 14A). It was assumed that if there was no interaction between the two eggs in the mixed pairs, their hatching time would be similar to the difference in the mean hatching time between the two controls (dotted line in Fig. 14A). It was reasonable to expect small hatching intervals when the two eggs in the mixed pairs had similar hatching times, as shown in Fig. 14A. However, their hatching intervals remained short (1–3 h), even when the two controls hatched 18 h apart or less, suggesting that the hatching timings were adjusted for synchronization. Hatching intervals tended to increase as the difference in mean hatching time between the two controls increased ($r = 0.94$, N = 14, $p < 0.001$), but the hatching intervals for the mixed eggs remained below the dotted line, suggesting that the hatching time of the mixed eggs modified even when the difference in development between the two controls exceeded 18 h (but less than 40 h). In this experiment, the time of the first hatching in each egg pod was designated as 1 h, and the mean hatching intervals of control 1 (15.3 h, N = 14) and 2 (17.7 h, N = 14) did not differ significantly from one another (Mann–Whitney's *U*-test; $p = 0.42$).
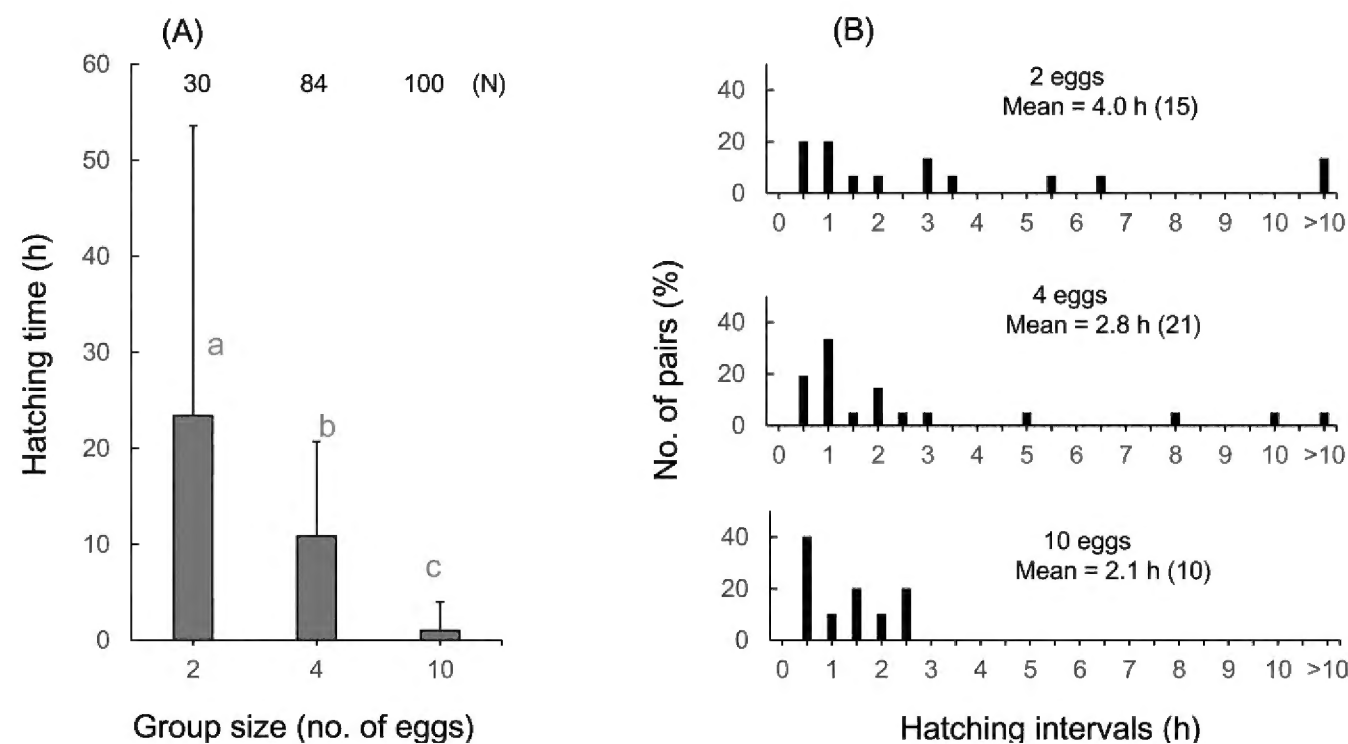
Fig. 11. Hatching times (**A**) and hatching intervals (**B**) of *Patanga japonica* eggs in different group sizes at 30°C. Different letters in (**A**) indicate significant differences at the 5% level by Tukey's multiple test. In (**B**), the numbers in parentheses indicate N, and no significant difference was observed in mean value between treatments by Steel-Dwass test at the 5% level.
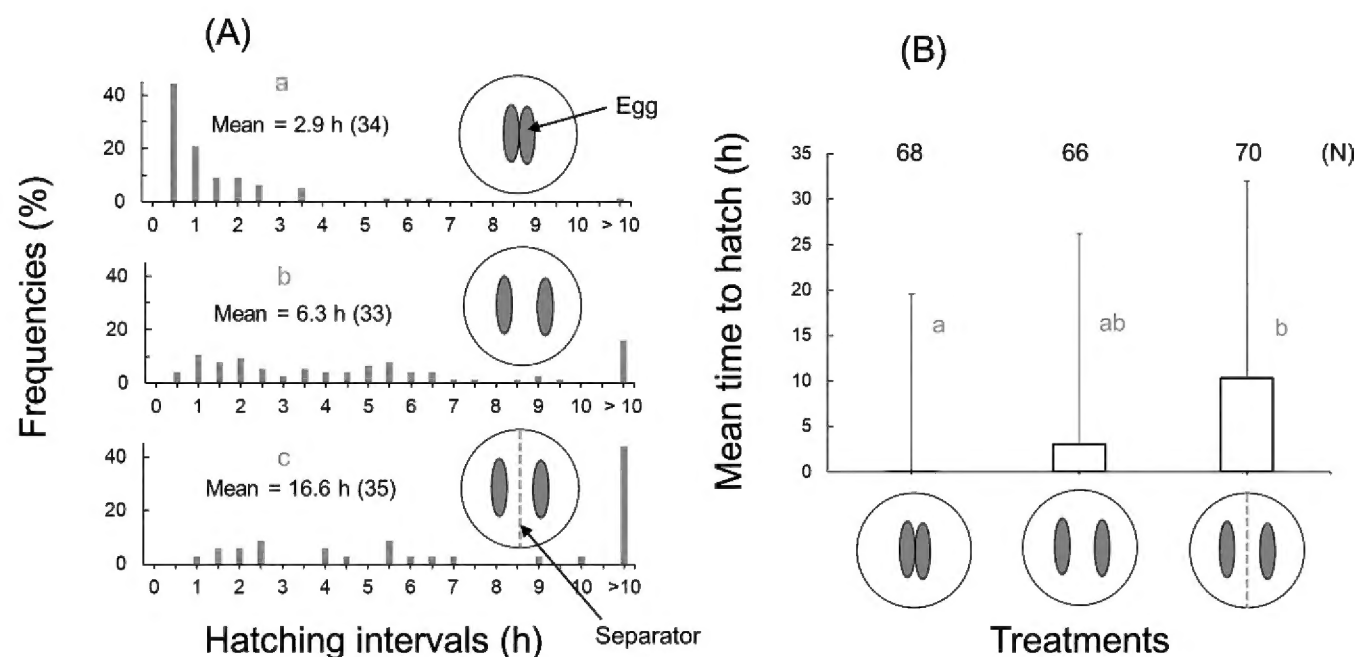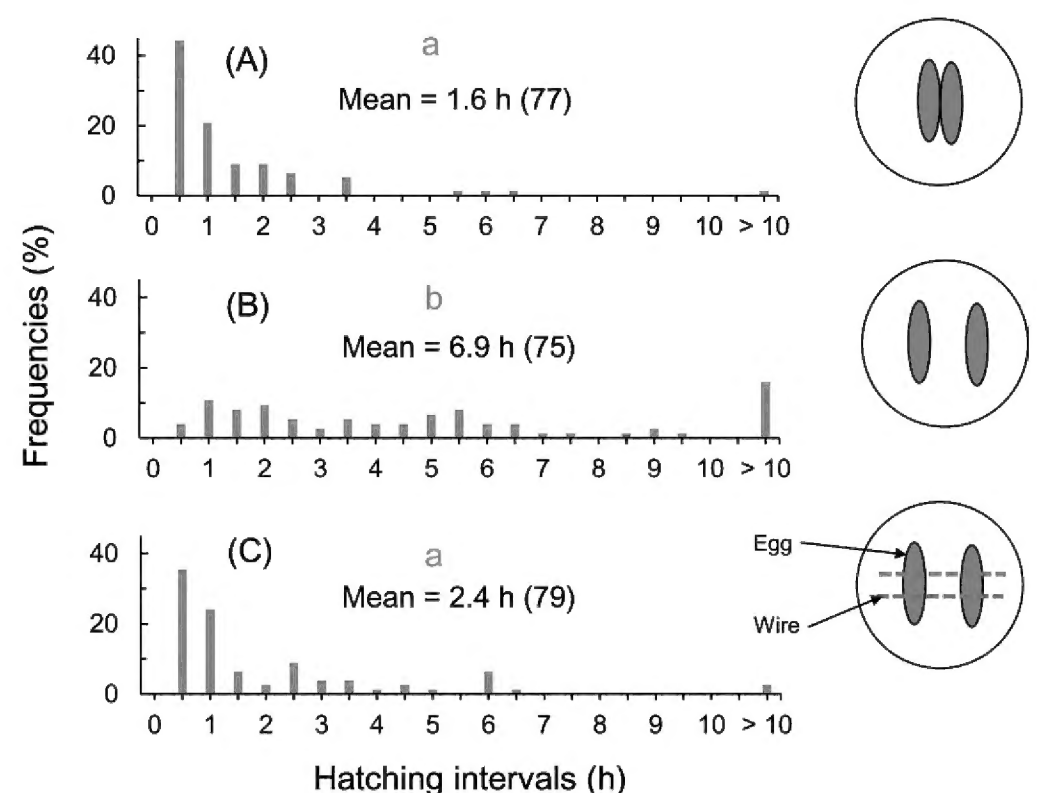

Fig. 12. Hatching intervals (**A**) and hatching times (mean + SD, B) in pairs of *Patanga japonica* eggs treated in different ways at 30°C as shown by diagrams. Different letters indicate significant differences at the 5% level by Steel-Dwass test in (**A**) and by Tukey's multiple test in (**B**). In (**A**), the numbers in parentheses indicate N.

For synchronous hatching to be achieved, egg hatching times must be adjusted. Fig. 14B gives an example showing that the early hatching eggs in the mixed pairs (mixed 1) delayed the hatching time for synchronization by 13.4 h, on average, compared with control 1 ($t = -2.27$, DF = 20, $p < 0.05$). In another experiment (Fig. 14C), the late hatching eggs in the mixed pairs (mixed 2) advanced the hatching time by 18.2 h, on average, compared with control 2 ($t = -2.19$, DF = 18, $p < 0.05$).

Adult morphology and crowding.—*P. japonica* adults collected before and after winter showed no significant difference in all body size dimensions measured for both sexes (Table 2), suggesting no significant size-dependent winter mortality. Therefore, the two datasets were combined in the following analyses.

Adults collected in the field (low density) and crowd-reared adults (high density) under outdoor conditions showed no significant difference in head width in either sex (Fig. 15A). The F/C ratio showed a tendency to increase in crowd-reared adults compared with those collected in the field (Fig. 15B), the direction of change being opposite to that observed in other locust species (Uvarov 1966). The E/F ratios showed an opposite tendency: crowding caused similar or reduced E/F ratios in both sexes (Fig. 15C). In

Fig. 13. Hatching intervals in pairs of *Patanga japonica* eggs treated in different ways at 30°C as shown by diagrams. Different letters indicate significant differences at the 5% level by Steel-Dwass test. The numbers in parentheses indicate N.
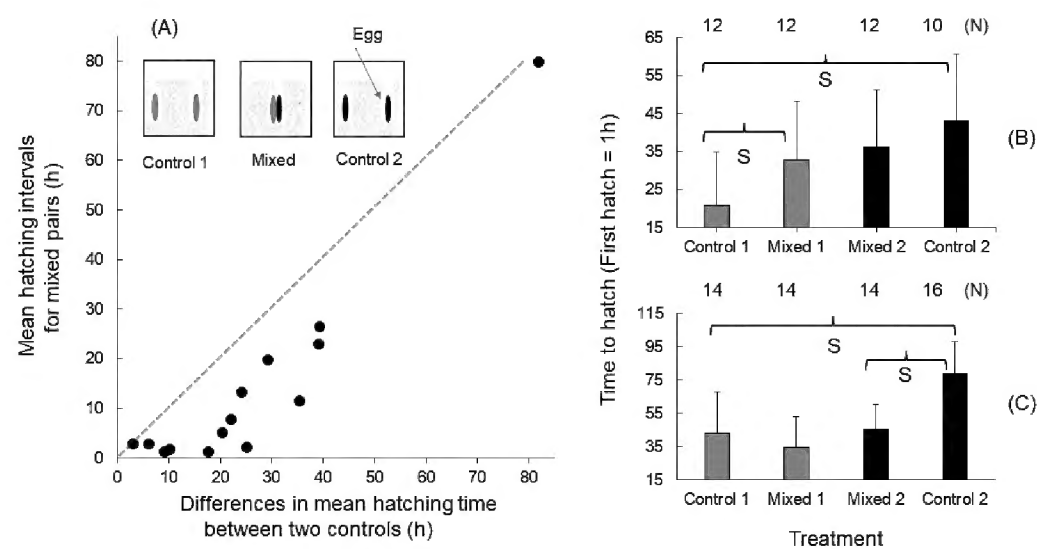
Fig. 14. Hatching intervals (**A**) and hatching times (**B, C**) of two *Patanga japonica* eggs buried individually (controls 1 and 2) or together (mixed) in sand at 30°C. In (**A**), diagram illustrates the experimental setup, and the dotted line indicates that two eggs in the mixed pairs had similar hatching times. The mean hatching time of mixed pairs was significantly accelerated (**A**) or delayed (**B**) compared with control eggs (s, $p < 0.05$; *t*-test).

regards to E/C ratio, the males that hatched on July 5 had a higher ratio than those that hatched on July 25 or those collected in the field (Fig. 15D). In females, this ratio in crowd-reared adults remained similar to that of the field-collected adults.

In adults reared indoors, head width was similar among males in different treatments irrespective of the rearing densities, whereas female adults reared singly in containers were significantly larger than those reared in a group in containers or cages (Tukey's multiple comparison, $p < 0.05$; Fig. 16A). The F/C ratio was similar among the three treatments, except for the males reared in a group of 50 individuals in cages, which showed a significantly larger value (Fig. 16B). The E/F ratio was significantly larger in males reared in a group of 5 than in the other treatments, and crowding caused no significant difference in the ratio in females (Fig. 16C). No significant difference was observed in E/C ratio in females, but the crowd-reared males showed a significantly larger E/C ratio than the males reared singly (Fig. 16D).

The proportions of adults with different shapes of pronotum in each sex were similar irrespective of rearing conditions (outdoors or indoors) or densities ($\chi^2 = 6.00$, DF = 4. $p > 0.05$ in females; $\chi^2 = 4.40$, DF = 4, $p > 0.05$ in males; Fig. 17). In males reared indoors in a group of 5 individuals per cup, there was only one individual with an arched-shaped pronotum. Therefore, the proportions of males with arched and flat pronota were combined to perform the above χ^2 tests. More concaved pronota and fewer arched pronota were observed in males than in females, and a significant sex difference was observed in the proportions of individuals with different shapes of pronotum in the three treatments (Fig. 17). However, neither rearing conditions (indoor or outdoor) nor density appeared to consistently explain the pattern observed.

Discussion

Seasonal life cycle and development.—The present study confirmed that *P. japonica* in central Japan has a univoltine life cycle. Nymphs started appearing early in the summer and emerged as adults in the fall. No adults reproduced before winter, and no new nymphs were observed in the field until the following July. Field observations, together with indoor rearing results, suggest that this species has 6 or 7 nymphal stadia. Preliminary observations suggest that significant sexual dimorphism in body size occurs at the third sta-
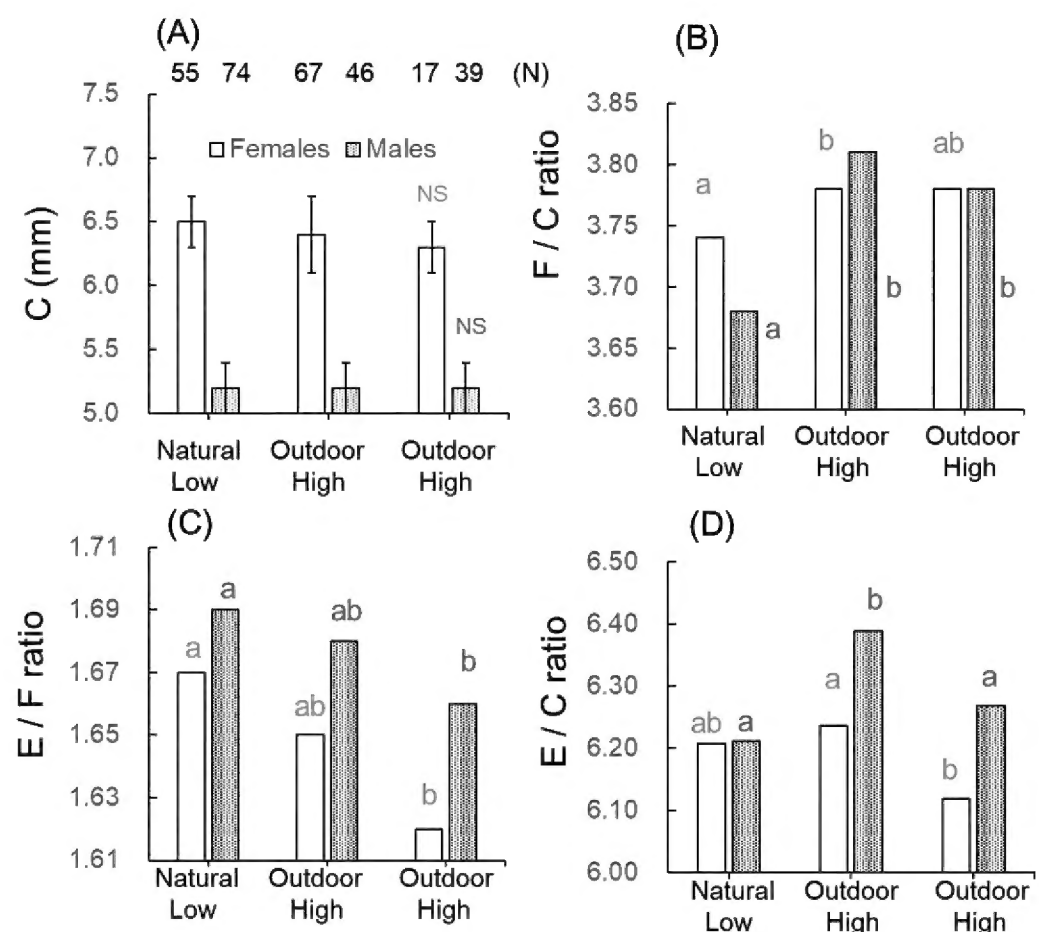
Fig. 15. Effects of growing density on (**A**) adult head width (mean ± SD), (**B**) femer length/head width, (**C**) forewing length/femur length and (**D**) forewing length/head width in *Patanga japonica* grown under natural (low density) or outdoor conditions (high density). Mean values were compared by Tukey's multiple comparison test in (**A**) and by Steel-Dwass test in (**B**), (**C**), and (**D**). Different letters indicate significant differences at the 5% level. NS indicates no significant difference. C, head width; F, femur length; E, forewing length. Adults in the two high-density groups hatched on July 5 and July 25, 2021 and were reared in a large cage in groups of approximately 200 and 100 individuals, respectively.

dium, and the two molting groups started showing a difference in body size at the fifth stadium: the mean head width was significantly smaller in the nymphs that underwent an extra molt than in the penultimate females but similar to the value in the penultimate males, including singly reared individuals (Suppl. material 1B). The former molted to larger last-instar nymphs than the latter. Only females underwent 7 nymphal stadia in the present observations, and this included the individuals reared singly.

New adults started appearing in mid-September, and most individuals emerged as adults by November. This was confirmed by outdoor rearing in a cage (Fig. 4). Interestingly, body size tended to increase as the time of adult emergence was delayed in females, whereas it remained similar in males. It is likely that this difference is partly a reflection of the sex differences in the number of nymphal stadia.

Males emerged as adults earlier than females, indicating protandry. Because this grasshopper does not reproduce before winter, the protandry may confer no advantage to males in terms of mating. Furthermore, adults of this grasshopper mate more than once during the adult stage. Thus, it is likely that the protandry in this grasshopper is a result of the body size difference between sexes. A similar situation might occur in solitarious *L. migratoria* in which protandry is also observed (H. Tanaka 1982). *L. migratoria* also shows polyandry, and the proportion of offspring sired by the last male to mate tends to be high (Tanaka and Zhu 2003). Therefore, the early adult emergence of males may not be so advantageous in terms of reproduction.

During the census, predatory animals were frequently encountered. They included mantises (*Tenodera aridifolia* (Stoll, 1813) and

Table 2. Morphological measurements of *Patanga japonica* adults collected in the field or reared under various conditions (A) and comparisons of body dimensions and morphometric ratios of adults collected before and after winter (B).

(A)

Sex	Growing conditions	Time of collection or rearing conditions	Females N	Mean ± SD (range) mm							Hatching date
				C	F	E	TBL	F / C	E / F	E / C	
Females											
	Natural	2020 Fall	38	6.5 ± 0.2 (6.0 – 7.1)	24.3 ± 0.8 (22.5 – 26.0)	40.7 ± 2.1 (35.7- 44.1)	51.6 ± 2.3 (45.3 – 55.5)	3.73	1.67	6.25	Unknown
	Natural	2021 Spring	17	6.6 ± 0.2 (6.2 – 7.0)	24.7 ± 1.2 (22.4 – 26.9)	40.9 ± 2.3 (37.2 – 44.9)	52.4 ± 2.8 (47.5 – 57.0)	3.76	1.65	6.18	Unknown
	Natural	Fall + Spring	55	6.5 ± 0.2 (6.0 – 7.0)	24.5 ± 0.9 (22.4 – 26.9)	40.7 ± 2.2 (35.7 – 44.9)	51.9 ± 2.6 (45.3 – 57.0)	3.74	1.67	6.21	Unknown
	Outdoor	Group-reared 1	67	6.4 ± 0.3 (5.7 – 7.1)	24.2 ± 1.1 (21.8 – 26.8)	40.0 ± 2.0 (35.7 – 44.9)	51.5 ± 2.7 (45.9 – 60.4)	3.78	1.65	6.24	5-Jul
	Outdoor	Group-reared 2	17	6.3 ± 0.2 (5.9 – 6.6)	23.8 ± 1.1 (20.8 – 25.6)	38.5 ± 1.8 (35.1 – 40.3)	49.6 ± 1.8 (46.0 – 51.6)	3.78	1.62	6.12	25-Jul
	Indoor	Group-reared 3	50	6.2 ± 0.3 (5.7 – 7.1)	23.2 ± 1.3 (21.2 – 263)	38.4 ± 1.8 (35.3 – 41.9)	49.2 ± 2.3 (45.6 – 54.5)	3.75	1.66	6.20	Jun 1 – Aug 14
	Indoor	Group-reared 4	45	6.2 ± 0.2 (5.8 – 6.6)	23.3 ± 0.8 (20.9 – 25.1)	38.7 ± 1.7 (35.5 – 42.0)	49.4 ± 1.9 (45.3 – 52.7)	3.77	1.66	6.26	May 31 – Jun 4
	Indoor	Isolation-reared	40	6.4 ± 0.2 (6.0 – 6.9)	24.0 ± 1.3 (21.4 – 27.8)	40.0 ± 1.8 (36.4 – 43.4)	50.8 ± 2.5 (42.3 – 55.9)	3.76	1.66	6.22	May 27 – June 4
Males											
	Natural	2020 Fall	50	5.2 ± 0.2 (4.7 – 5.5)	19.1 ± 0.7 (17.2 – 20.3)	32.4 ± 0.9 (29.6 – 34.2)	41.7 ± 0.1 (38.3 – 43.8)	3.67	1.70	6.22	Unknown
	Natural	2021 Spring	24	5.2 ± 0.2 (4.8 – 5.5)	19.2 ± 0.8 (17.4 – 21.0)	32.1 ± 1.4 (29.1 -34.5)	41.3 ± 1.7 (37.6 – 44.0)	3.69	1.67	6.17	Unknown
	Natural	Fall + Spring	74	5.2 ± 0.2 (4.7 – 5.5)	19.1 ± 0.7 (17.2 – 21.0)	32.3 ± 1.1 (29.1 -34.5)	41.6 ± 1.4 (37.6 – 44.0)	3.68	1.69	6.21	Unknown
	Outdoor	Group-reared 1	46	5.2 ± 0.2 (5.0 -5.6)	20.1 ± 1.1 (18.5 – 25.0)	33.7 ± 1.5 (31.1 – 37.0)	43.5 ± 1.7 (39.9 – 47.2)	3.81	1.68	6.39	5-Jul
	Outdoor	Group-reared 2	39	5.3 ± 0.2 (5.0 – 5.8)	20.1 ± 0.6 (18.9 – 21.6)	33.5 ± 1.0 (31.4 – 35.6)	43.2 ± 1.3 (40.9 – 46.4)	3.78	1.66	6.30	25-Jul
	Indoor	Group-reared 3	49	5.2 ± 0.2 (4.9 – 5.6)	19.7 ± 0.9 (18.1 – 22.3)	33.6 ± 1.4 (30.4 – 37.7)	43.0 ± 2.2 (39.3 – 52.5)	3.78	1.70	6.43	Jun 1 – Aug 14
	Indoor	Group-reared 4	52	5.2 ± 0.2 (4.9 – 5.8)	20.1 ± 0.9 (18.2 – 23.3)	33.6 ± 1.5 (30.7 – 36.8)	43.2 ± 1.8 (39.0 – 47.0)	3.84	1.67	6.41	May 31 – Jun 4
	Indoor	Isolation-reared	32	5.2 ± 0.2 (4.9 – 5.6)	20.0 ± 0.7 (18.7 – 21.3)	32.3 ± 2.3 (22.6 – 35.8)	42.5 ± 2.2 (39.3 – 51.5)	3.76	1.64	6.18	May 27 – June 4

(B)

Sex	Test	mm							
		C	F	E	TBL	F / C	E / F	E / C	
Females	t-test or Mann-Whitney's *U*-test	$t = -1.49$	$t = -1.8$	$t = -0.33$	$t = -1.02$	$z = -0.11$	$z = -1.70$	$z = -1.04$	
	p value	0.14	0.07	0.75	0.31	0.913	0.089	0.299	
Males	t-test or Mann-Whitney's *U*-test	$t = 0.52$	$t = -0.37$	$t = 0.91$	$t = 0.96$	$z = -1.11$	$z = -1.60$	$z = -0.525$	
	p value	0.60	0.72	0.37	0.35	0.268	0.110	0.525	

T. angustipennis (Saussure, 1869)), dragonflies (*Orthetrum albistylum speciosum* (Uhler, 1858)), ants, paper wasps, spiders (*Trichonephila clavata* (L. Koch, 1878)), lizards (*Plestiodon japonicus* (Peters, 1864) and *Takydromus tachydromoides* (Schlegel, 1838)), tree frogs (*Dryophytes japonica* (Günther, 1859)), and birds. However, I only witnessed one *P. japonica* nymph caught by a *T. aridifolia* nymph and one nymph and one adult trapped by the webs of *T. clavata*.

Host plants.—*P. japonica* has been known to feed on various plants, including *P. montana var. lobata, Humulus scandens*, and grasses (Ichikawa et al. 2006). However, no quantitative data on the host plants of this grasshopper have been reported for this grasshopper. In the present study, nymphs and adults were observed on *P. montana var. lobata, M. sinensis, I. cylindrica*, and other plants. While most individuals were observed on the first three plant species, the proportion of adult individuals on the other plants was larger than the proportion of nymphs. This difference was probably not due to the difference in the plants they fed on but rather to behavioral differences: adults often stayed on non-feeding plants, such as *Solidago canadensis* var. *scabra* (Muhl. ex Willd.) Torr. & A. Gray and *Conyza canadensis* (L.) Cronquist, whereas nymphs primarily stayed on feeding plants.

Out of the 51 plant species that were collected in the habitats of *P. japonica*, 37 (73%) were consumed by nymphs, and at least one individual (out of 5) molted to the second stadium. The three plants—*P. montana var. lobata, M. sinensis*, and *I. cylindrica*—which were most frequently observed with *P. japonica* at the study site, supported the development of most or all nymphs to the second stadium. In the present study, the test nymphs were given only single plant species, and the test was discontinued upon ecdysis to the second stadium. Therefore, how many plant species can support the full development of this grasshopper remains unknown. In nature, *P. japonica* is likely to use a limited number of host plants because of their preference. The range of host plants would be different in different flora habitats. During the present study, I visited another habitat of *P. japonica* where nymphs were mainly observed on *E. crus-galli, H. scandens,* and *Setaria viridis* (L.) P. Beauv., which are the dominant plant species in the area. It is
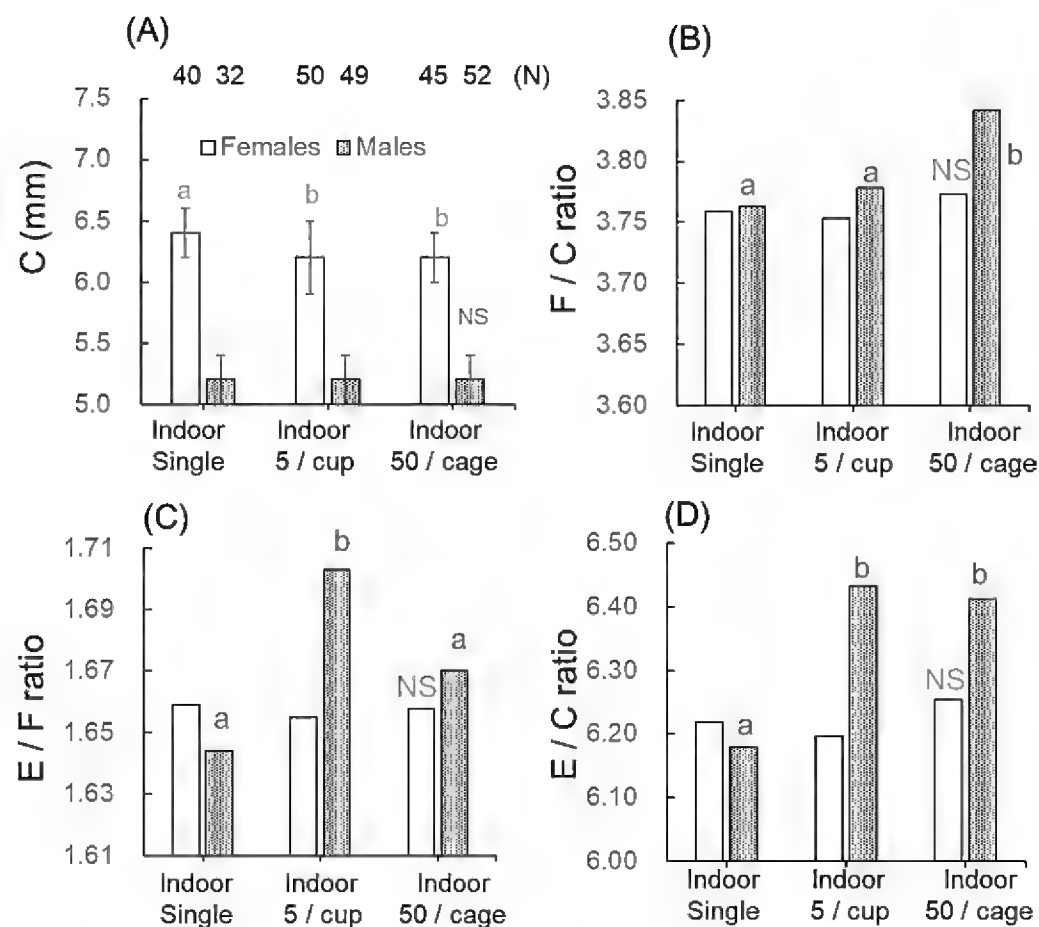
Fig. 16. Effects of growing density on (**A**) adult head width, (**B**) femur length/head width, (**C**) forewing length/femur length, and (**D**) forewing length/head width in *Patanga japonica* grown under indoor conditions. Nymphs were reared singly, in a group of 5 per cup, or in a group of 50 per cage. Mean values were compared by Tukey's multiple comparison test in (**A**) and by Steel-Dwass test in (**B**), (**C**), and (**D**). Different letters indicate significant differences at the 5% level. NS indicates no significant difference. C, head width; F, femur length; E, forewing length.

also likely that they use different plant species in different seasons, even in the same habitat. Nevertheless, the present study documented that this grasshopper could use a wide variety of plant species to develop.

Mating behavior.—Overwintered *P. japonica* adults started mating in the spring. In outdoor cages, mating was observed frequently in April and May. As mentioned earlier, most mounting pairs were copulating, suggesting that pre-copulatory mounting was very short in this grasshopper, unlike other species (Parker 1970, Parker and Smith 1975, Zhu and Tanaka 2002, Tanaka and Zhu 2003). Adults became very rare in the field in July.

Under outdoor conditions, the number of copulating pairs tended to increase during the day, and the daily maximum number of copulating pairs correlated with the mean daily temperature. In this study, the length of copulation was not determined precisely, but it varied greatly from less than 1 h to 14 h from 08:00 to 22:00. Some marked pairs were observed copulating during 2 or 3 consecutive observation periods (08:00–18:00), suggesting that copulation might last for 2 or 3 days if copulation continued without interruption during the night.

As observed in other grasshoppers (Uvarov 1966), males of *P. japonica* mount a female and copulate by reaching their penis to her genitalia. In this case, the males reach the females' genitalia from either side. The number of males reaching from the right or left was similar. In the mantis *T. aridifolia*, males all reach the female genitalia from her right side (Ando 2021). If a right-reaching (or left-reaching) male of *P. japonica* was removed from the copulating female and introduced to a second female, he reached her genitalia from the same side, even when the previous male that had mated with her was left-reaching (or right-reaching).

However, the male's behavior in this is probably not fixed but flexible. Males with one hindleg missing copulated with a female from the side of the missing leg. This may be related to the male's stridulation behavior that is observed during copulation. Males rubbed a hind tarsus against their forewing or abdomen 3 or 4 times consecutively and repeated this behavior while copulating (Suppl. material 4). Therefore, this stridulation may be categorized as a copulation song (Uvarov 1977). It seems that the function of this stridulation is to calm down the partner while copulating. The male with a missing hindleg had to use the remaining leg for stridulation, which may explain why such a male copulated with a female from the side of the missing hindleg: because he needed to be able to balance for stridulation. In one case, I observed a male that lacked the tarsus of his right hindleg. He copulated with a female as if the whole right hindleg had been missing: he reached her from the right side and stridulated using his left hindleg. Future studies should confirm the existence of this behavior by removing one hindleg or tarsus from a male and observing how he copulates. In the present study, no pre-copulatory behavior was investigated.

Oviposition.—In a survey of 163 grasshopper species, 85% laid their eggs in soil, 7% laid them on plants, 5% laid them in plants, and 4% laid them in detritus (Stauffer and Whitman 1997). *P. japonica* females deposit their egg pods in soil. Judging from the sites where hatchlings appeared in the field, eggs were laid in vegetation areas where the ground was partially exposed. Under outdoor conditions, oviposition began in late April and continued until the beginning of August. Peak oviposition activity occurred in June. Egg pods contained 72.1 eggs on average. Because female adults had an average of 124 ovarioles, they use only 58.1% of their ovarioles for egg production, which is similar to the value for solitarious females of migratory locust (62.8%, N = 470, Tanaka, S. unpublished observation).

Egg size is influenced by various physical and biological factors (Stauffer and Whitman 1997, Whitman 2008). As often observed in other insects (Honěk 1993, Davidowitz 2008, Yanagi and Tuda 2012), larger females of *P. japonica* appeared to have more ovarioles and lay more eggs per pod. However, unlike other insects showing a positive correlation (Atkinson and Begon 1987, 1988, Davidowitz 2008), *P. japonica* showed no significant correlation between female body size and egg size. A negative correlation or trade-off between egg size and number is common in insects (Branson 2008, Whitman 2008). A similar relationship was observed between the number of eggs per pod and egg length in *P. japonica*. In the present study, no attempt was made to investigate the evolutionary significance of egg size variations.

Hatching and the mechanism controlling hatching synchrony.—Under outdoor conditions, egg hatching in *P. japonica* occurred during the daytime, but the eggs of each pod hatched simultaneously. Hatching during the daytime is common in grasshoppers (Tanaka 2021b). In the desert locust, however, eggs kept under 12-h photocycles or thermocycles hatch during the dark or cryoperiod (low temperature period) rather than during the light or thermoperiod (Padgham 1981, Nishide et al. 2015a, b). In the field, they hatch over a brief period from shortly before dawn to the first 4 h after sunrise (Ellis & Ashall, 1957). In *L. migratoria* under laboratory conditions, eggs also hatch in response to temperature and photoperiod (Nishide et al. 2015b). In the field, however, eggs are buried in soil and rely on changes in temperature alone to control hatching time (Nishide et al. 2015b, 2017a). It would be interesting to explore on a molecular basis why and how this locust perceives and uses light to control hatching time. In *L. migratoria*, the eggs hatched between 09:00 and
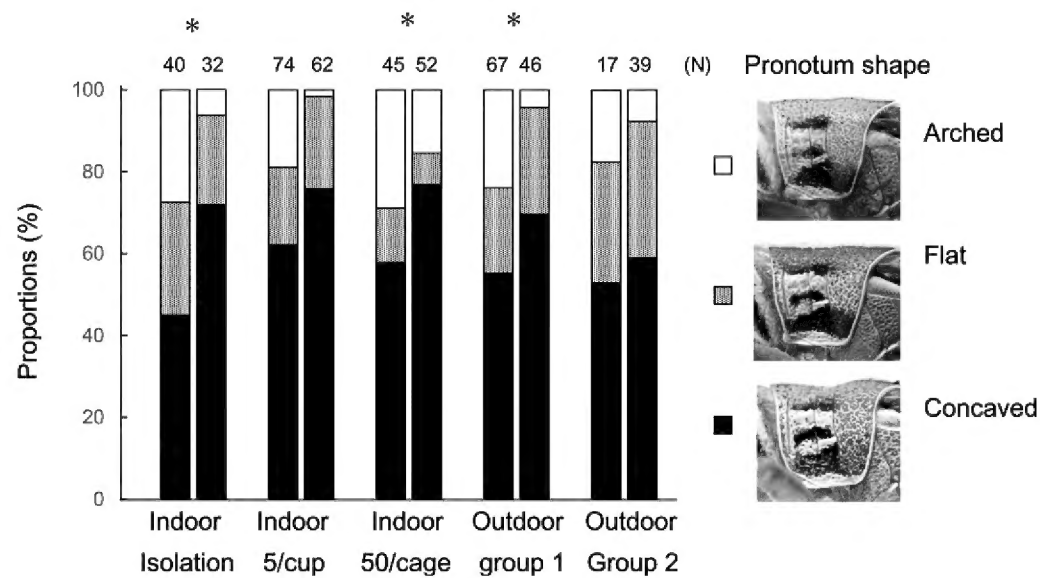
Fig. 17. Variation in adult pronotum shape in *Patanga japonica* reared singly or in groups under indoor or outdoor conditions. Photographs on the right show different shapes of pronotum. Individuals in group 1 and 2 hatched on July 5 and July 25 in 2021 and were reared in a group of approximately 200 and 100 in a large cage, respectively. Asterisks indicate a significant difference between sexes by χ^2 test ($p < 0.05$).

16:00 in the field (Chen 1999, Nishide et al. 2017b). *P. japonica* eggs also hatched during the day under outdoor conditions. However, no detailed analysis was carried out on the hatching time of this grasshopper in relation to temperature or other factors.

Hatching synchrony of *P. japonica* was confirmed to occur at a constant temperature of 30°C. In this case, only eggs buried as a group in sand hatched in synchrony, while those individually buried in sand hatched sporadically over a longer period. Hatching synchrony was achieved even in pairs of eggs kept in contact with one another. Greater increases in group size did not bring about significant changes in the hatching interval. However, hatching became earlier as group size increased. Two explanations for this phenomenon, which are not mutually exclusive, have been suggested: 1) A larger egg group is more likely to contain an early-hatching egg and 2) there are group-size dependent embryo–embryo interactions that might control hatching time (Tanaka 2021a). Two eggs separated by several millimeters on sand hatched less synchronously than those kept in contact with one another, but hatching synchrony occurred when the similarly separated eggs were connected by a steel wire, suggesting that physical stimuli transmitted via the wire induced hatching synchrony.

A similar phenomenon is known in other grasshoppers and locusts, and embryo–embryo interactions are involved in controlling hatching synchrony (Nishide and Tanaka 2016, Tanaka 2017, 2021a, b, Tanaka et al. 2018, Sakamoto et al. 2019). In *L. migratoria*, two eggs that would have otherwise hatched more than one day apart hatched together when kept in contact with one another (Tanaka 2017). To achieve synchronous hatching, egg hatching time had to be adjusted. In *L. migratoria* and the Bombay locust, *Patanga succincta* (Johannson, 1763), the hatching time of eggs is either delayed or advanced depending on the development of adjacent eggs. In contrast, the hatching time of the eggs of *S. gregaria* only advance to achieve synchronous hatching (Tanaka 2021a). The present study suggests that *P. japonica* is similar to the former.

In the field, newly hatched nymphs of *P. japonica* were observed climbing up *P. montana var. lobata* quickly and forming small aggregations of 3–7 individuals on the leaves (Suppl. material 2F). They appeared to be quite sensitive to vibrational or visual stimuli because they quickly scattered in all directions when I came close to them for

photographing. Similar behaviors were observed in other grasshoppers. In *R. microptera* and *T. eques,* newly hatched nymphs quickly aggregate, sometimes forming a tight, touching ball of 10–40 nymphs. In *T. eques*, these tight aggregations break apart by the second stadium, but in *R. microptera*, they may continue into the third stadium. When such a ball of touching nymphs is approached, the nymphs jump wildly in every direction (Whitman DW, pers. comm.). This kind of behavior suggests that one of the functions of synchronous hatching is to form an aggregation to escape from approaching predators, as suggested for *P. succincta* (Tanaka 2021b). Synchronous hatching is also likely to reduce the probability of detection by predators by limiting the duration of hatching from the pod. Eggs buried separately in sand showed a lower rate of hatchability than those buried in a group. These observations suggest the possibility that group hatching facilitates successful egg hatching and might have influenced the evolution of egg deposition in an egg pod in grasshoppers.

Adult body size and crowding effects.—In the temperate region of Japan, *P. japonica* is the only grasshopper species known to overwinter as an adult (Ichikawa et al. 2006). A comparison of adults collected before and after winter suggested that there was no size-dependent mortality during winter. This grasshopper also overwinters in the adult stage in the subtropical region and maintains a univoltine life cycle (Ichikawa et al. 2006, Murai and Ito 2011). However, there is a large difference in adult body size between temperate and subtropical populations. For example, the female and male mean head widths of an Okinawa population are 9.0 cm (range, 9.5–8.5 mm; N = 31) and 6.9 mm (7.2–6.3 mm; N = 41), respectively (Tanaka and Okuda 1996), whereas the corresponding figures for the Tsukuba population are 6.5 cm (6.0–7.0 mm; N = 55) and 5.2 cm (4.7–5.5 mm; N = 74) (Table 1). Despite the large difference in body size, large females from a subtropical population copulated with small males from a temperate population in a small cage (Tanaka and Okuda 1996). Whether such pairing produces viable eggs, however, is unknown. In a small cage, a *P. japonica* female and a male of another species, *P. succincta*, collected in Okinawa, were observed copulating (Suppl. material 7), although no such heterospecific mating pair was observed when more than 40 mating pairs were examined at a sugarcane field in 1990 where the two species occurred sympatrically (Tanaka S, unpublished observation). In contrast, the incubation period of eggs at 30°C is approximately 7 days longer in the Okinawa population than in the Tsukuba population of *P. japonica* (Tanaka and Okuda 1996, and this study). It would, therefore, be worthwhile to confirm the species status of the temperate and subtropical populations.

Density-dependent changes in morphometric ratios are one of the most important characteristics of phase polyphenism (Uvarov 1966, 1977, Pener 1991, Pener and Yerushalmi 1998, Pener and Simpson 2009). Two species of locusts, *S. gregaria* and *L. migratoria*, are typical examples showing such changes, and the F/C and E/F ratios of these species are frequently used to separate individuals in different phases (Dirsh 1951, 1953, Farrow and Colless 1980, H. Tanaka 1982, Yerushalmi et al. 2001, Hoste et al. 2002 2003, Tanaka et al. 2002, Yamagishi and Tanaka 2009, Sugahara et al. 2015, 2016). In the above two locusts, crowding causes the F/C ratio to decrease and the E/F ratio to increase. Similar changes have been observed in *P. succincta* in Okinawa (Yasuda 1986). In *P. japonica*, these ratios also tended to be influenced by crowding, but the direction of the changes was opposite to what was expected.

The E/C ratio showed an interesting response to crowding, tending to increase in males but not in females. This ratio is higher in long-winged individuals than in short-winged ones in *L. migratoria* (Tanaka and Nishide 2013, Nishide and Tanaka

2013) and *S. gregaria* (Sugahara et al. 2017). If the ratio reflects flight capability, it might follow that *P. japonica* males emerge as better fliers under high population density than under low population density. Under outdoor conditions, this ratio increased in one of the crowd-reared treatments in which most adults emerged in September when the temperature was still relatively high and might be favorable for flight activity. To understand the significance of this response, further research should investigate the other factor(s) that are responsible for the changes in E/C ratio and dispersal activity in this grasshopper.

The pronotum shape is another character known to change density dependently in *L. migratoria* (Uvarov 1966, Tanaka et al. 2002). In *P. japonica*, a significant difference was observed in the proportions of arched, flat, and concave pronota between sexes, but there was no evidence indicating the presence of a density-dependent change in this trait.

As is often observed in locusts (Pener 1991), *P. japonica* nymphs become heavily melanized under crowded conditions (Tanaka and Okuda 1996), and this phenomenon was also observed during the present study (details to be published). Unlike locusts, however, nymphs of *P. japonica* were considerably inactive, even under crowded conditions, and no increased locomotor activity was seen, although no attempts were made to quantify their activities. Crowding is also known to induce a difference in egg size in locusts (Hunter-Jones 1958, Uvarov 1966, Nishide and Tanaka 2019). In *P. japonica*, however, crowding caused a reduction in egg number but not in egg size. In the temperate area, no records indicate the formation of aggregation or swarming in this species, except for small aggregations of hatchlings observed at low-population density. However, the available information suggests that *P. japonica* exhibits density-dependent polyphenism in some characters, as observed in locusts.

Acknowledgements

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Supplementary material 1

Author: Seiji Tanaka
Data type: JPEG file
Explanation note: Nymphal growth (head width, mean ± SD mm) of *Patanga japonica* under outdoor conditions. Nymphs were reared in a group from June to August (A) and from August to September (B). In (B) males, females and females that underwent an extra molt and their mean head widths (± SD) are shown separately as black, red, and green bars or letters, respectively. A few days after each molt, nymphs were measured, marked with white paint on a hind femur, and transferred to another cage. Roman numerals indicate the stadia. Numbers in parentheses indicate N. Significant differences were observed in mean head width among the three groups of last instar nymphs by Tukey's multiple test ($p < 0.05$). F, female; M, male; O, penultimate instar: L, last instar.

Link: https://doi.org/10.3897/jor.32.95753.suppl1

Supplementary material 2

Author: Seiji Tanaka
Data type: JPEG file
Explanation note: Wood-framed enclosure for grasshopper behavior observations; B. Small cages; C. Setup for observing hatching time; D. Feeding mark; E. Mating postures; F. Small aggregation of hatchlings.

Link: https://doi.org/10.3897/jor.32.95753.suppl2

Supplementary material 3

Author: Seiji Tanaka
Data type: JPEG file
Explanation note: Lengths of copulation under outdoor conditions in *Patanga japonica*. Observations were made from April 21 to April 25 in 2022. X-axis indicates the lengths of copulation recorded during the daily observation period (08:00–18:00 or 22:00). Pairs that were still mating at the end of daily observation are labeled 'copulation continued'.

Link: https://doi.org/10.3897/jor.32.95753.suppl3

Supplementary material 4

Author: Seiji Tanaka
Data type: movie
Explanation note: Video showing a typical mating and stridulation by a *Patanga japonica* male.

Link: https://doi.org/10.3897/jor.32.95753.suppl4

Supplementary material 5

Author: Seiji Tanaka
Data type: movie
Explanation note: Slow-motion video showing stridulation behavior by a male on a female of *Patanga japonica*. The female body was tilted by approximately 30 degrees to orient their body towards the sun and the male used both legs for stridulation.

Link: https://doi.org/10.3897/jor.32.95753.suppl5

Supplementary material 6

Author: Seiji Tanaka
Data type: JPEG file
Explanation note: Oviposition intervals in *Patanga japonica* in outdoor cages (A) and cumulative number of females that deposited the last egg pod on the indicated date (B) in 2021. In (A), mean ± SD is given.

Link: https://doi.org/10.3897/jor.32.95753.suppl6

Supplementary material 7

Author: Seiji Tanaka
Data type: JPEG file
Explanation note: Heterospecfic mating of *Patanga japonica* female and Bombay locust *Patanga succincta* male (A). Note that the eye stripes are conspicuous only in *P. succincta* (B).

Link: https://doi.org/10.3897/jor.32.95753.suppl7